

ENDEMISM IN NEOTROPICAL PODOSTEMACEAE¹

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ABSTRACT

Podostemaceae, a family of plants restricted to river rapids and waterfalls, are widely reported to have a high degree of local species endemism. We tested this idea for Neotropical members of the family using historical records, herbarium holdings, personal field collections, and geographic information systems analyses. In contrast to estimates of endemism based on the landmark studies of P. van Royen (66%), we report 15%–37% based on current taxonomy. Examples of regional endemism, based on extent of occurrence and longest geographic axis measures, are discussed for a subset of species. Major hydrographic regions (Amazon River System, Paraná River System) and major areas (eastern Brazil) are shown to possess largely unique podostemad floras. We propose rivers and river systems as the most appropriate units to assess endemism for Podostemaceae, and consider one-river and two-river endemics as narrowly distributed. Limitations in the current taxonomy are discussed relative to establishment of meaningful estimates of local species endemism. We provisionally apply IUCN assessment categories to Neotropical Podostemaceae and report that approximately one third of the species fall into one of three categories: Data Deficient (DD), Least Concern (LC), and Vulnerable (VU). Ten species are Critically Endangered (CR). Species of Podostemaceae are restricted to an environment that has experienced major human impacts—tropical rivers. Large dams make long reaches of rivers inhospitable. Expanded use of hydropower in Latin America will exacerbate the problem.

RESUMO

Podostemaceae, uma família botânica restrita a ambientes de corredeiras e cachoeiras, é amplamente reportada como de espécies com alto grau de endemismo local. Testamos esta hipótese para os representantes neotropicais da família, utilizando os dados históricos da literatura, material depositado em herbário, coletas empreendidas pelos autores e uma análise através do sistema de informação geográfica. Em contraste com a estimativa de endemismo referenciada nos estudos de P. van Royen (66%), reportamos 15%–37% de espécies endêmicas, baseadas na taxonomia atual. Exemplos de endemismo regional, suportados pela amplitude de ocorrência e de maior eixo geográfico são discutidos para um subgrupo de espécies. Grandes regiões hidrográficas (Bacia do rio Amazonas, Bacia do rio Paraná) e grandes áreas (sudeste do Brasil), demonstraram possuir uma ampla e distinta flora de Podostemaceae. Propomos rios e bacias como a unidade mais apropriada para acessar o endemismo de Podostemaceae, considerando endêmicas de um-rio e de dois-rios como distribuição restrita. Limitações no conhecimento taxonômico atual são discutidas com relação ao estabelecimento de uma estimativa significativa de endemismo local de espécies. Aplicamos provisoriamente o estado de conservação de espécies neotropicais de Podostemaceae de acordo com as categorias da IUCN, reportando que aproximadamente um terço das espécies se encaixa em uma das seguintes categorias: Dados Insuficientes (DD), Não Ameaçada (LC) e Vulneráveis (VU). Dez espécies estão Criticamente Ameaçadas (CR). As espécies de Podostemaceae são restritas a ambientes que têm sofrido os maiores impactos antrópicos—os rios tropicais. Grandes reservatórios tornam grandes extensões dos rios inabitáveis. A expansão do uso de energia proveniente de hidrelétricas na América Latina irão exacerbar este problema.

Key words: Aquatic plant, endemism, hydropower, IUCN Red List, large dam, Podostemaceae.

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Podostemaceae are the largest family of strictly aquatic flowering plants. Approximately 20 genera and more than 150 species in this pantropical family are reported from the Neotropics (Royen, 1951, 1953, 1954; Cook, 1996a). Plants occur attached to solid substrata in swift currents of river rapids and waterfalls. There has been a resurgence of interest in the family over the past two decades. Considerable work has focused on interpreting the unusual morphology and development of vegetative structures (e.g., Rutishauser, 1997; Ameka et al., 2003; Jäger-Züm, 2005), phylogenetic placement of the family (e.g., Gustafsson et al., 2002; Wurdack & Davis, 2009), and infrafamilial phylogenetic patterns (e.g., Kita & Kato, 2001, 2004; Moline et al., 2007; Tippery et al., in press). The present study addresses another aspect of the family—species endemism.

Weddell (1872) and Willis (1902, 1914) were among the earliest to discuss the prevalence of narrow species distributions in the family. For example, Willis (1914: 545) stated that species "...are usually very local in distribution." He noted that species of *Castelnavia* Tul. & Wedd. (Brazil) are endemic to few waterfalls: "...some of the species differ at every cataract." Royen (1951: 13) reflected the same idea: "According to descriptions given by botanists each cataract and each set of rapids would have its own species." It is commonly stated in the literature that Podostemaceae have a high proportion of species with narrow distributions (e.g., Royen, 1951; Taylor, 1953; Sculthorpe, 1967; Graham & Wood, 1975; Philbrick & Novelo, 1995, 2004; Cook, 1996a, b; Ameka, 2000; Rutishauser & Pfeifer, 2002; León, 2006; Cook & Rutishauser, 2007). The present authors, however, are not aware of any detailed analysis of the taxonomic or geographic extent of endemism in Podostemaceae.

Analyses of distribution patterns, and thereby initial assessments of species endemism, are based on taxonomic studies. The most comprehensive taxonomic studies of Neotropical Podostemaceae were by Royen (1951, 1953, 1954). His works indicate that many species were known from few collections; a remarkable number were "once collected" (Royen, 1951, 1953, 1954). Possible relationships between species that had only been collected once and those that are actually endemic to narrow regions remain uncertain. Although more than 50 years of systematic study have occurred since Royen's works, the topic of species endemism remains largely unaddressed. Herein we consider this issue and provide the first detailed assessment of narrow species distributions (i.e., endemism) in Neotropical Podostemaceae.

Tropical rivers are under intense threat by humans (e.g., Nilsson & Berggren, 2000; Pringle et al., 2000; WWF International, 2004). For example, dam build-

ing in Latin America has had dramatic negative impacts on river biota (e.g., Pringle et al., 2000; Poff & Hart, 2002). With few exceptions, Podostemaceae are restricted to tropical rivers. Consequently, it is important to assess the degree of narrow species endemism such that possible conservation concerns can be identified and addressed.

The current study has several objectives. First, provide an updated list of Neotropical species and an overview of their geographic distributions. Second, establish the scale and incidence of species endemism. In doing so, the landmark papers of Royen (1951, 1953, 1954) will be used to develop a standard against which to compare insights gained over the past five decades. Geographic information systems (GIS) will be used to assess the distributions of a subset of Neotropical species based on the number of river systems and rivers they occupy. Three general issues relating to conservation will also be considered: (1) the importance of river systems and rivers, as opposed to specific sites, for assessing the distribution of these riverine species; (2) application of IUCN Red List categories for estimating the degree of extinction threat faced by species; and (3) the significance of large dams as a pervasive threat to Podostemaceae in the Neotropics.

METHODS

Two estimates of endemism were produced. The first was derived from information provided exclusively in Royen's (1951, 1953, 1954) treatment of Podostemaceae in the New World. Although Royen (1951, 1953, 1954) recognized forms and varieties for some species, only species-level taxonomy is discussed here as subspecific taxa are difficult to identify. Geographic distributions of species recognized by Royen (1951, 1953, 1954) were based exclusively on voucher specimens he listed.

Estimates were then calculated based on the current taxonomy, i.e., Royen (1951, 1953, 1954) and taxonomic studies published subsequently (Schnell, 1969; Royen & Reitz, 1971; Tur, 1975, 1987, 1997, 2003; Burger, 1983; Hollander & Berg, 1983; Novelo & Philbrick, 1993a, b, 1995, 1997; Werkhoven & Peeters, 1993; Velásquez, 1994; Philbrick & Novelo, 2001, 2004; Philbrick, 2002; Berry, 2004; Philbrick et al., 2004a, b, 2009; Bove et al., 2006, in press; Rial & Bove, 2007; Philbrick & Bove, 2008). We also used information derived from holdings in the following herbaria: BBS, C, CAR, EAP, GH, GUA, ICN, L, MEXU, MG, NHA, NY, R, RB, U, VEN, WCSU.

Podostemaceae are restricted to rivers. We propose that the number of rivers in which a species occurs is

Table 1. Number of river systems (number of rivers in parentheses) from which 22 representative species and two taxonomic forms were documented from each of five hydrogeographic regions. These data are a summary of Appendix 3.

	Amazon River System	Eastern Brazil Area	Guiana Area	Orinoco River System	Paraná River System	EOO (km ²)
<i>Castelnavia fluitans</i>	3 (7)	0	0	0	0	321,772
<i>C. monandra</i>	1 (1)	0	0	0	0	41
<i>C. multipartita</i> f. <i>multipartita</i>	3 (6)	0	0	0	0	162,683
<i>C. multipartita</i> f. <i>pendulosa</i>	2 (3)	0	0	0	0	29,019
<i>C. noveloi</i>	1 (1)	0	0	0	0	10
<i>C. princeps</i>	3 (6)	1 (2)	0	0	1 (3)	1,566,044
<i>Ceratolacis pedunculatum</i>	0	1 (4)	0	0	0	6010
<i>Cipoia inserta</i>	1 (4)	3 (9)	0	0	0	118,706
<i>C. ramosa</i>	0	1 (1)	0	0	0	10
<i>Diamantina lombardii</i>	0	3 (3)	0	0	0	3069
<i>Lophogyne</i> sp. A	0	7 (10)	0	0	0	74,677
<i>Monostylis capillacea</i>	3 (10)	0	0	0	0	880,715
<i>Podostemum comatum</i>	0	0	0	0	6 (13)	535,545
<i>P. distichum</i>	0	0	0	0	12 (44)	1,164,242
<i>P. flagelliforme</i>	1 (1)	0	0	0	0	10
<i>P. irgangii</i>	0	0	0	0	1 (2)	20,536
<i>P. muelleri</i>	0	0	0	0	8 (33)	461,353
<i>P. ovatum</i>	0	4 (7)	0	0	0	28,087
<i>P. rutifolium</i> subsp. <i>rutifolium</i>	0	0	0	0	8 (47)	781,899
<i>P. saldanhanum</i>	0	3 (4)	0	0	0	50
<i>P. scaturiginum</i>	1 (3)	4 (6)	0	0	1 (3)	290,965
<i>P. weddellianum</i>	0	12 (34)	0	0	1 (6)	205,454
<i>Weddellina squamulosa</i>	7 (19)	0	7 (8)	1 (5)	0	4,352,897

the most appropriate geographic context against which to judge species distributions. Documenting a species at one location within a river is a reliable predictor that the species will occur elsewhere in that river. A species documented from only a single river, regardless of the number of collections from that river, is scored as a “one-river endemic.” Similar procedures were followed to determine two-river endemics.

Analyses of species distributions within and between (1) main areas and hydrographic regions, (2) river systems, and (3) rivers were conducted for 22 representative species in eight genera (*Castelnavia*, *Cipoia* C. T. Philbrick, Novelo & Irgang, *Ceratolacis* Wedd., *Diamantina* Novelo, C. T. Philbrick & Irgang, *Lophogyne* Tul., *Monostylis* Tul., *Podostemum* Michx., *Weddellina* Tul.) (Table 1). Species selected were clearly circumscribed taxonomically, with geographic distributions that were relatively well documented. The species included occur primarily south of the Amazon River, ranging from central to southeastern Brazil, Argentina, Uruguay, and Paraguay. Only a single species (*Weddellina squamulosa* Tul.) was included that ranged into northern South America. Voucher specimens are cited in Appendix 1 or derived from the relevant published literature (Phil-

brick & Novelo, 2004; Philbrick et al., 2004a, b, 2009; Bove et al., 2006, in press).

The hydrographic regions and/or main areas demarcated by Ziesler and Ardizzone (1979) were assessed relative to the 22 representative species noted above. The majority of species occurred in one of three hydrographic regions or areas: Amazon River System, Eastern Brazil Area, and Paraná River System. Two additional regions (Guiana Area, Orinoco River System) were considered relative to one species (*Weddellina squamulosa*). Within each of these regions, rivers that shared the same outflow were defined as “river systems.” The name used for each river system was that for the largest river.

Two sources of information directly influence estimates of endemism: new information on species distributions and taxonomic change. Documentation of broader species distributions than previously known is clearly important. Field studies can reveal that a species once thought to be restricted to a single location has a broader distribution. Taxonomic change is also important, e.g., species once considered endemic may be placed in synonymy under more widespread species or new species being described.

Preliminary assessments for the extinction threat of species (current taxonomy only) are provided. It was

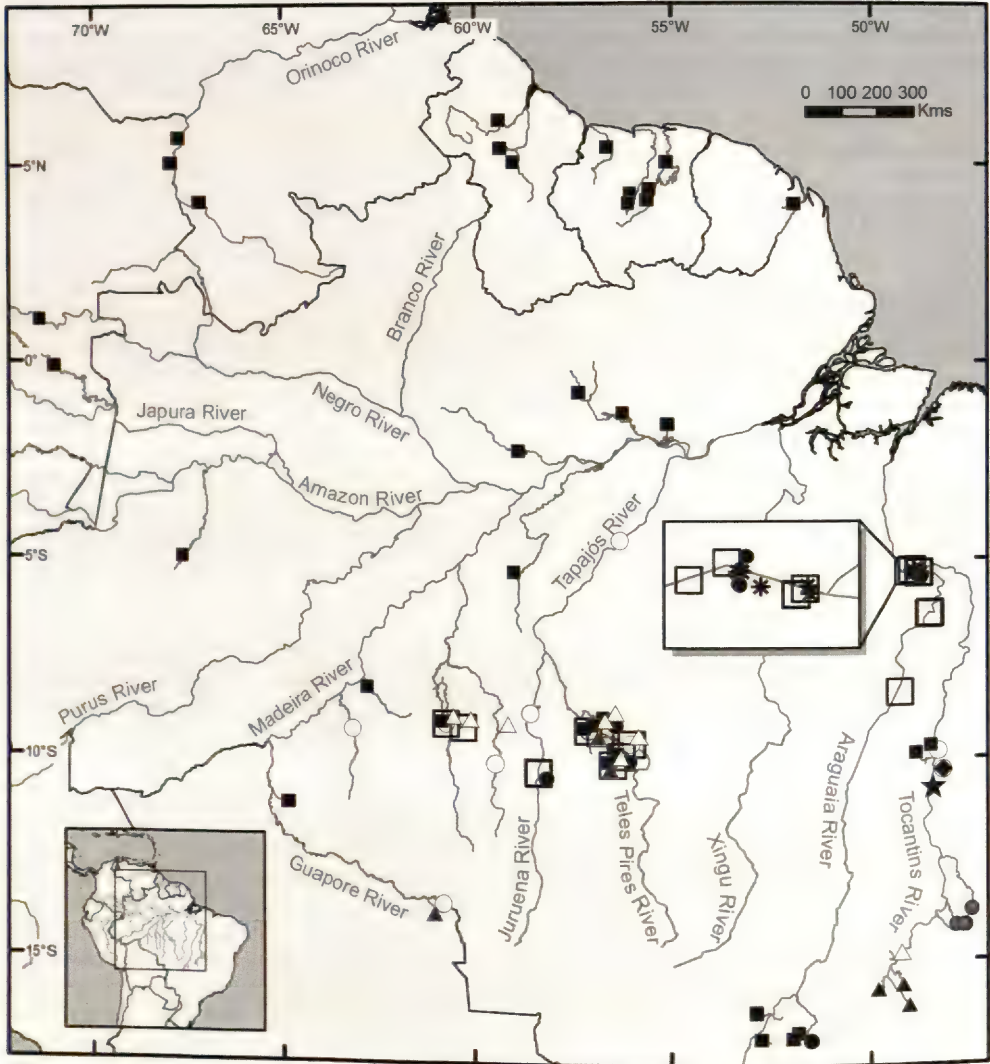


Figure 1. Distribution of 10 species and one taxonomic form of Podostemaceae in three hydrographic regions or major areas as demarcated by Ziesler and Ardizzone (1979): Amazon River System, Orinoco River System, Guiana Area. Representative large river names are included. Inset shows a region of the Tocantins River where *Castelnavia fluitans*, *C. monandra*, and *C. princeps* occur. Open square, *Castelnavia fluitans*; asterisk, *C. monandra*; open triangle, *C. multipartita* f. *multipartita*; gray triangle, *C. multipartita* f. *pendulosa* C. T. Philbrick & Bove; diamond, *C. noveloi*; filled circle, *C. princeps*; gray circle, *C. inserta*; open circle, *Monostylis capillacea*; star, *Podostemum flagelliforme*; filled triangle, *P. scaturiginum*; filled square, *Weddellina squamulosa*.

not possible to directly assess the degree and type of human impacts on each species. Consequently, assessments for most species were based on numbers of rivers in which a species occurs. The IUCN Red List categories (IUCN, 2009; <<http://www.iucnredlist.org/>>) were used when sufficient information was available regarding their geographic distribution and taxonomy.

Twenty-two species were mapped and analyzed using GIS software (ArcMap 9.3). River systems were delineated following the hydrographic zones demarcated by Ziesler and Ardizzone (1979) and using geospatial rivers data from The Americas Base Map (Bletter et al., 2004). Both the major and minor rivers depicted (Figs. 1–3) were chosen based on the occurrence of taxa of interest and for cartographic

clarity. Specimen data coordinates were assumed to be in the World Geographic System (WGS) 1984. Extent of occurrence (EOO), a criterion used for IUCN Red List analysis (IUCN, 2009) that measures the area of a minimum convex polygon drawn around a set of occurrences, was calculated for all species that had distributions in three or more unique localities using Hawth's Tools Minimum Convex Polygon tool (Beyer, 2004). Three species (*Castelnavia noveloi* C. T. Philbrick & C. P. Bove, *Cipoia ramosa* C. P. Bove, C. T. Philbrick & Novelo, and *Podostemum flagelliforme* (Tul. & Wedd.) C. T. Philbrick & Novelo) were each documented by one collection. Consequently, EOO for each of these was estimated as 10 km². All spatial data were projected to the South America Albers Equal Area Conic coordinate system for EOO calculations.

IUCN (2009) categories were applied to each species. All species, except the 22 representative species listed above, documented from three or fewer rivers were scored as Vulnerable (VU). Such a designation reflects the restricted number of rivers from which a species is known. Species documented from four or more rivers were scored as Least Concern (LC). It is realized that the three versus four river distinction between VU and LC categories is arbitrary. Even so, this distinction is heuristic for the issues discussed herein. Species were scored as Endangered (EN) or Critically Endangered (CR) for one of two reasons: (1) if the species was previously scored as EN or CR in the published literature (cf. Bove et al., in press; León, 2006) and subsequent information was not available; (2) if during our field studies a given target species was sought, but not found, in the only region where it had been previously documented. For the 22 representative species analyzed with GIS (see above), a combination of river number and EOO (IUCN, 2009) criteria were used. Species with EOO values of < 100 km² and < 20,000 km² were scored as CR and VU, respectively.

It is important to note our strong reservations regarding the taxonomic validity of many species recognized in the current published literature. Many of these species have been distinguished based on minor vegetative and/or floral differences (e.g., leaf length, ultimate leaf division size or form, anther length). We believe that recognition of such species reflects an unreasonably narrow species concept given the degree of variation that we have observed (often on a single plant) while conducting field studies (i.e., Argentina, Brazil, Costa Rica, Honduras, Mexico, Paraguay, Suriname, Venezuela) over the past 15 years. Whether these species remain worthy of taxonomic recognition after detailed study, or should be placed in synonymy with other species, remains to be determined. Species whose taxonomic status we

interpret as tentative and in need of further study are scored as Data Deficient (DD).

Estimates of the length of reservoirs associated with hydroelectric dams were made using the ruler tool on Google Earth (<<http://earth.google.com/>>; 16 June 2008). While these estimates are rough, they provide a reliable approximation of minimum reservoir length and are sufficient for issues discussed herein.

RESULTS

ROYEN'S TAXONOMY AND ESTIMATES OF ENDEMISM

Royen (1951, 1953, 1954) recognized 19 genera and 152 species (Table 2, Appendix 2). Genus size ranged from a single species (*Ceratolacis*, *Devillea* Tul. & Wedd., *Lonchostephus* Tul., *Macarenia* P. Royen, *Monostylis*, *Tristicha* Thouars, *Tulasneantha* P. Royen, *Weddellina*) to 48 species (*Apinagia* Tul.). Sixteen of the 19 genera recognized by Royen included at least a single one-river endemic species (Table 2). The percentage of one-river endemism per genus ranged from zero in three genera (*Lophogyne*, *Tristicha*, *Weddellina*) to 100% in six (*Ceratolacis*, *Devillea*, *Lonchostephus*, *Macarenia*, *Monostylis*, *Wettsteinia* Suess.). Five of the six genera with 100% one-river endemism were monotypic, while *Wettsteinia* had two species. The three largest genera (*Apinagia*, *Marathrum* Bonpl., *Rhyncholacis* Tul.) had 56%, 21%, and 48% one-river endemism, respectively. It is notable that eight of the nine species (89%) of *Castelnavia* were also one-river endemics. Overall, 73 (48%) of the species recognized by Royen were one-river endemics (Table 2).

Six genera contained at least a single two-river endemic species (Table 2). *Apinagia* (10) had the most. *Rhyncholacis* had five, while *Jenmaniella* Engl., *Marathrum*, *Mourera* Aubl., and *Podostemum* each had three. Twenty-seven species were two-river endemics. In Royen's treatments, 100 (66%) of the species recognized were either one- or two-river endemics.

CURRENT TAXONOMY AND ESTIMATES OF ENDEMISM

Synopsis of current taxonomy. Twenty genera and 135 species were recognized by us in the current taxonomy (Table 2, Appendix 2). Nine genera were monotypic (*Diamantina*, *Lonchostephus*, *Lophogyne*, *Macarenia*, *Monostylis*, *Tristicha*, *Tulasneantha*, *Varroyenella* Novelo & C. T. Philbrick, *Weddellina*), and *Apinagia* had the largest number of species (51). We did not accept two genera recognized by Royen (1951, 1953, 1954; *Mniopsis* Mart., *Devillea*) and included

Table 2. Comparison of taxonomy of Royen (1951, 1953, 1954) with current taxonomy. For each genus, the number of species recognized is listed along with the number of one- and two-river endemic species. For current taxonomy, number of species scored as Data Deficient (DD) is also listed. See text for discussion. n.a., Genus not recognized.

Genus	Royen (1951, 1953, 1954)			Current taxonomy				
	No. of species	One-river endemic	Two-river endemic	No. of species	One-river endemic	Data Deficient	Two-river endemic	Data Deficient
<i>Apinagia</i>	48	27 (56%)	10 (21%)	51	22 (43%)	19 (86%)	9 (41%)	1 (11%)
<i>Castelnavia</i>	9	8 (89%)	0	5	2 (40%)	0	0	0
<i>Ceratolacis</i>	1	1 (100%)	0	2	1 (50%)	0	0	0
<i>Cipoia</i>	n.a.	n.a.	n.a.	2	1 (50%)	0	0	0
<i>Devillea</i>	1	1 (100%)	0	n.a.	n.a.	n.a.	n.a.	n.a.
<i>Diamantina</i>	n.a.	n.a.	n.a.	1	0	0	0	0
<i>Jenmaniella</i>	7	3 (43%)	3 (43%)	7	3 (43%)	3 (100%)	2 (29%)	2 (100%)
<i>Lonchostephus</i>	1	1 (100%)	0	1	0	0	0	0
<i>Lophogyne</i>	2	0	0	1	0	0	0	0
<i>Macarenia</i>	1	1 (100%)	0	1	1 (100%)	0	0	0
<i>Marathrum</i>	19	4 (21%)	3 (16%)	10	2 (20%)	0	2 (20%)	1 (50%)
<i>Mniopsis</i>	5	2 (40%)	0	n.a.	n.a.	n.a.	n.a.	n.a.
<i>Monostylis</i>	1	1 (100%)	0	1	0	0	0	0
<i>Mourera</i>	6	1 (17%)	3 (50%)	6	1 (17%)	1 (100%)	2 (33%)	1 (50%)
<i>Oserya</i>	6	4 (67%)	0	7	5 (71%)	4 (80%)	0	0
<i>Podostemum</i>	17	5 (29%)	3 (18%)	11	1 (9%)	0	1 (9%)	1 (100%)
<i>Rhyncholacis</i>	23	11 (48%)	5 (22%)	22	7 (32%)	7 (100%)	6 (27%)	1 (17%)
<i>Tristicha</i>	1	0	0	1	0	0	0	0
<i>Tulasneantha</i>	1	1 (100%)	0	1	1 (100%)	0	0	0
<i>Vanroyenella</i>	n.a.	n.a.	n.a.	1	0	0	1 (100%)	0
<i>Weddellina</i>	1	0	0	1	0	0	0	0
<i>Wettsteiniola</i>	2	2 (100%)	0	3	3 (100%)	1 (33%)	0	0
Totals	152	73 (48%)	27 (18%)	135	50 (37%)	35 (70%)	22 (16%)	7 (30%)

three new genera described since his monographs (*Cipoia*, *Diamantina*, *Vanroyenella*).

Published literature: geographic distribution of species. Schnell (1969, Guyana) reported broader geographic ranges than Royen (1951, 1953, 1954) for several species of *Apinagia* (*A. divertens* Went ex Pulle, *A. guyanensis* (Pulle) P. Royen, *A. longifolia* (Tul.) P. Royen, *A. marowynensis* (Went) P. Royen, *A. richardiana* (Tul.) P. Royen, *A. secundiflora* Pulle), as well as *Marathrum capillaceum* (Pulle) P. Royen and *Oserya perpusilla* (Went) P. Royen. Berry (2004, Venezuela) documented the occurrence of species in several genera that Royen (1951, 1954) did not report for the country: *Apinagia* (*A. longifolia*, *A. guyanensis*, *A. staheliana* (Went) P. Royen, *A. corymbosa* (Tul.) Engl., *A. exilis* (Tul.) P. Royen), *Marathrum* (*M. squamosum* Wedd.), *Oserya* Tul. & Wedd. (*O. perpusilla*), *Rhyncholacis* (*R. hydrocichorium* Tul., *R. applanata* K. I. Goebel, *R. flagellifolia* P. Royen), *Weddellina* (*W. squamulosa*). Berry (2004) also listed distributional information for nine species in four genera that indicated broader distributions than reported by Royen (1951, 1954): *A. kochii* (Engl.) P. Royen, *A. multibranchiata* (Matthiesen) P. Royen, *A.*

ruppioides Tul., *Jenmaniella ceratophylla* Engl., *M. capillaceum*, *O. perpusilla*, *R. coronata* P. Royen, *R. divaricata* Matthiesen, *R. penicillata* Matthiesen. Lastly, Berry (2004) confirmed the narrow distribution of some species as reported by Royen (1951), e.g., *A. brevicaulis* Mildbr. and *M. aeruginosum* P. Royen.

Werkhoven and Peeters (1993, Suriname) presented floristic data for 24 species in seven genera. Information provided for 15 species differs little from Royen (1951, 1953, 1954): *Apinagia divertens*, *A. hulkiana* (Went) P. Royen, *A. longifolia*, *A. richardiana*, *A. secundiflora*, *A. staheliana*, *A. treslingiana* (Went) P. Royen, *A. versteegiana* (Went) P. Royen, *Marathrum capillaceum*, *Oserya minima* P. Royen, *O. perpusilla*, *Rhyncholacis cristata* P. Royen, *R. dentata* P. Royen, *Tristicha trifaria* (Bory ex Willd.) Spreng., and *Weddellina squamulosa*. They also listed *A. secundiflora* and *R. cristata* as restricted to the Suriname River, which corresponded to Royen (1951).

Two species that Royen (1951) documented from a single collection each were listed as more widespread by Werkhoven and Peeters (1993): *Apinagia imthurnii* (K. I. Goebel) P. Royen and *A. penicillata* (P. Royen) P. Royen. Four species of *Apinagia* listed by Werkhoven and Peeters (1993) for Suriname had not

previously been documented for the country by Royen (1951): *A. digitata* P. Royen, *A. flexuosa* (Tul.) P. Royen, *A. guyanensis*, and *A. marowynensis*.

Tur (1997, Argentina) reported that *Podostemum muelleri* Warm. and *P. rutifolium* Warm. occurred in Argentina, while Royen (1954) did not. Although Tur (1997) reported other species of *Podostemum* (e.g., *P. comatum* Hicken) as restricted to small areas, the revised taxonomy of the genus provided by Philbrick and Novelo (2004; see below) presented a markedly different view of species distributions.

Novelo and Philbrick (1997, Mexico) documented the following species to be more widespread in Mexico than reported by Royen (1951, 1954): *Marathrum tenue* Liebm., *M. foeniculaceum* (as *M. schiedeanum* Cham.), and *Oserya coulteriana* Tul. Moreover, *O. longifolia* Novelo & C. T. Philbrick was endemic to one river in Jalisco, while *Vanroyenella plumosa* Novelo & C. T. Philbrick occurred in two rivers, one each in the states of Jalisco and Oaxaca.

Philbrick and Novelo (2004, *Podostemum*) reported that several species of *Podostemum* had wider geographic ranges than reported by Royen (1954), e.g., *P. distichum* (Cham.) Wedd. and *P. rutifolium* subsp. *rutifolium*. In their studies, both Royen and Philbrick and Novelo indicated that *P. flagelliforme* (Tul. & Wedd.) C. T. Philbrick & Novelo (previously treated by Royen as *Devillea flagelliformis* Tul. & Wedd.) occurred only in a single river.

Podostemum flagelliforme was the only species in the genus that was documented from a single location. Several other species, however, had narrow geographic ranges. For example, *P. weddellianum* (Tul.) C. T. Philbrick & Novelo occurred only within the Brazilian states of Minas Gerais, Rio de Janeiro, Espírito Santo, and São Paulo. *Podostemum ovatum* C. T. Philbrick & Novelo was only known from northeast São Paulo, Rio de Janeiro, and central Espírito Santo, while *P. irgangii* C. T. Philbrick & Novelo had been documented from a small region of Santa Catarina and adjacent Paraná. *Podostemum saldanhanum* (Warm.) C. T. Philbrick & Novelo, which occurred singly in the central part of the state of Rio de Janeiro, had the second narrowest distribution of species in the genus after *P. flagelliforme*.

Philbrick et al. (2009) recognized five species of *Castelnavia*, two of which were one-river endemics. *Castelnavia monandra* Tul. & Wedd. occurred along an approximately 25-km region of the Araguaia River, while the present known distribution of *C. noveloii* spanned a 0.5–1 km length of the Taquaruçu River in south-central Tocantins State. In contrast, two of the remaining species (*C. fluitans* Tul. & Wedd. and *C. multipartita* Tul. & Wedd.) were documented from more than six rivers each and ranged across an

approximately 1400-km region in south-central Brazil. *Castelnavia princeps* Tul. & Wedd. was the most widespread species in the genus, occurring in more than 10 rivers in Goiás, Mato Grosso, Minas Gerais, Pará, and Tocantins.

Velásquez (1994, Venezuela) listed 10 species for the country that were not reported by Royen (1951, 1954), e.g., *Apinagia longifolia*, *A. secundiflora*, *Marathrum squamosum*, and *Oserya perpusilla*. Two species that Royen (1951) listed from a single location (*A. multibranchiata*, *A. ruppioides*) were documented by Velásquez (1994) to occur at more locations. It is notable that *A. corymbosa* and *A. brevicaulis* were reported for Venezuela by Royen (1951) and Berry (2004), but not by Velásquez (1994).

Published literature: new taxa. Thirteen new species were published from the Americas since Royen (1951, 1953, 1954) (Appendix 2). Schnell (1969) and Hollander and Berg (1983) described one *Apinagia* species each, the former from Guyana (*A. itanensis* Schnell) and the latter from Suriname (*A. petiolata* Hollander). Six new species were described from Brazil, all from central or southern regions. Philbrick and Bove (2008) described *Castelnavia noveloii* from Tocantins. Philbrick et al. (2004a) described the genus *Cipoia* (*C. inserta* C. T. Philbrick, Novelo & Irgang), while Bove et al. (2006) published a second species (*C. ramosa*) for the genus. Single species were also published for *Ceratolacis* (*C. pedunculatum* C. T. Philbrick, Novelo & Irgang; Philbrick et al., 2004b) and *Diamantina* (*D. lombardii* Novelo, C. T. Philbrick & Irgang; Philbrick et al., 2004a). Lastly, *Podostemum irgangii* (Philbrick & Novelo, 2001) was documented from Paraná and Santa Catarina.

Three new species were described from Mexico: *Marathrum rubrum* Novelo & C. T. Philbrick (Novelo & Philbrick, 1993a), *Oserya longifolia* (Novelo & Philbrick, 1995), and *Vanroyenella plumosa* (Novelo & Philbrick, 1993b). (Novelo et al. [2009] subsequently placed *M. rubrum* in synonymy under *M. foeniculaceum* Humb. & Bonpl.). Lastly, two new species have been described from Argentina: *M. azarensis* Tur (Tur, 2003) and *Wettsteiniola apipensis* Tur (Tur, 1975).

Several nomenclatural changes were also made. *Podostemum ovatum* is a new name that was published during this period, but does not represent a new species (see Philbrick & Novelo, 2004, *Mniopsis glazioviana* Warm.). Cook and Rutishauser (2001) transferred species of *Mniopsis* Mart. to *Crenias* Spreng.

Published literature: names placed in synonymy. The number of species in several genera has been

reduced relative to Royen (1951, 1953, 1954; Appendix 2). Burger (1983) questioned the validity of several species of *Marathrum* reported for Costa Rica. Novelo et al. (2009), in their treatment of Podostemaceae for *Flora Mesoamericana*, synonymized eight species of *Marathrum* previously recognized by Royen (1951) under their broadened concept of *M. foeniculaceum*.

Philbrick and Novelo (2004) proposed a broader interpretation of the genus *Podostemum* than Royen (1954), combining *Devillea* and *Crenias* (*Mniopsis*) with *Podostemum*. The species concept employed by Philbrick and Novelo (2004) was also markedly expanded. Royen (1954) recognized 23 species (and six varieties) of *Podostemum* (including *Devillea* and *Crenias*), while Philbrick and Novelo (2004) reported 11 species and two subspecies in the single genus *Podostemum*. Philbrick et al. (2009) proposed five species of *Castelnavia*, compared to the nine recognized by Royen (1954). Lastly, Bove et al. (in press) reduced the number of species recognized in *Lophogyne* from two to one.

Insight from herbarium holdings. Examination of herbarium holdings (Appendix 1) indicated broader distributions for many species than reported by Royen (1951, 1953, 1954). Royen (1954) reported *Monostylis capillacea* Tul. and *Lonchostephus elegans* Tul. only from the Amazon River in the Brazilian state of Pará. Herbarium holdings documented a broader distribution for both. The former exhibited a broader range in Brazil (Mato Grosso, Rondônia, Tocantins; also see below) and also occurred in Bolivia (Santa Cruz). The latter species was also documented from Mato Grosso and Tocantins (Brazil).

Some species of *Apinagia* and *Oserya* were more widely distributed than previously reported. *Apinagia peruviana* (Wedd.) Engl. occurred in Ecuador, although Royen (1951) had listed it from only Peru. Werkhoven and Peeters (1993) reported that *A. nana* Went, a species not recognized by Royen (1951), occurred in two river systems in Suriname. Field collections by one of us (Philbrick) indicated that this species is abundant in Suriname and Venezuela, as is *O. perpusilla* (Appendix 1).

Even species that Royen reported as common in some regions have been shown to have much wider geographic distributions. Royen (1953) indicated *Weddellina squamulosa* occurred north of the Amazon River (northern Brazil, Colombia, Venezuela, Guyana, Suriname). Field and herbarium studies indicated that it ranges south of the Amazon River in Brazil in Goiás, Mato Grosso, Rondônia, and Tocantins (Appendix 1; also see below). *Marathrum utile* Tul., a species previously reported from Venezuela and Colombia to

Costa Rica, has also been documented from Honduras.

SPECIES DISTRIBUTIONS (GIS): MAJOR AREAS, HYDROGRAPHIC BASINS, RIVER SYSTEMS, RIVERS

Distributions for 22 species documented using GIS varied in terms of the number of major areas, hydrographic basins, river systems, and rivers in which they occurred (Table 1, Figs. 1–3, Appendix 3). Eleven species occurred in the Amazon River System hydrographic basin (Fig. 1), with seven taxa restricted to the region: *Castelnavia fluitans*, *C. monandra*, both forms of *C. multipartita*, *C. noveloi*, *Monostylis capillacea*, and *Podostemum flagelliforme*. *Castelnavia fluitans*, *C. multipartita* (both taxonomic forms), and *Monostylis capillacea* were documented from the Madeira, Tapajós, and Tocantins river systems, where they occurred in at least six rivers. Three of the species restricted to the Amazon River System hydrographic basin (*C. monandra*, *C. noveloi*, *P. flagelliforme*) were documented only from the Tocantins River System; all three were single-river endemics. *Castelnavia monandra* and the apparently extinct *P. flagelliforme* (cf. Philbrick & Novelo, 2004) were documented from the Araguaia River. *Castelnavia noveloi* occurred only in the Taquaruçu River, a tributary of the Tocantins River. Four species that occurred in the Amazon River System hydrographic basin also occurred in other major areas or hydrographic basins (see below). The number of species per river system ranged from one to nine. The Tocantins River System was the most species rich (10 species), followed by the Madeira and Tapajós river systems (six species each).

Eight species occurred in the Paraná River System hydrographic basin (Table 1, Fig. 2, Appendix 3), with five taxa restricted there: *Podostemum comatum*, *P. distichum*, *P. irgangii*, *P. muelleri*, and *P. rutifolium* subsp. *rutifolium*. *Podostemum distichum* and *P. rutifolium* subsp. *rutifolium* spanned greater than 40 rivers each; the former in 12 and the latter in eight river systems. In contrast, *P. comatum* had a narrower distribution (six river systems, 13 rivers), while *P. irgangii* was known from a single river system and two rivers. None of the species that occurred in the Paraná River System were single-river endemics. Three species documented from the Paraná River System also occurred in other major areas or hydrographic basins (see below). The Paraná hydrographic system contained the most species (seven), closely followed by the Uruguay River System with five. The remaining river systems had one to four species each.

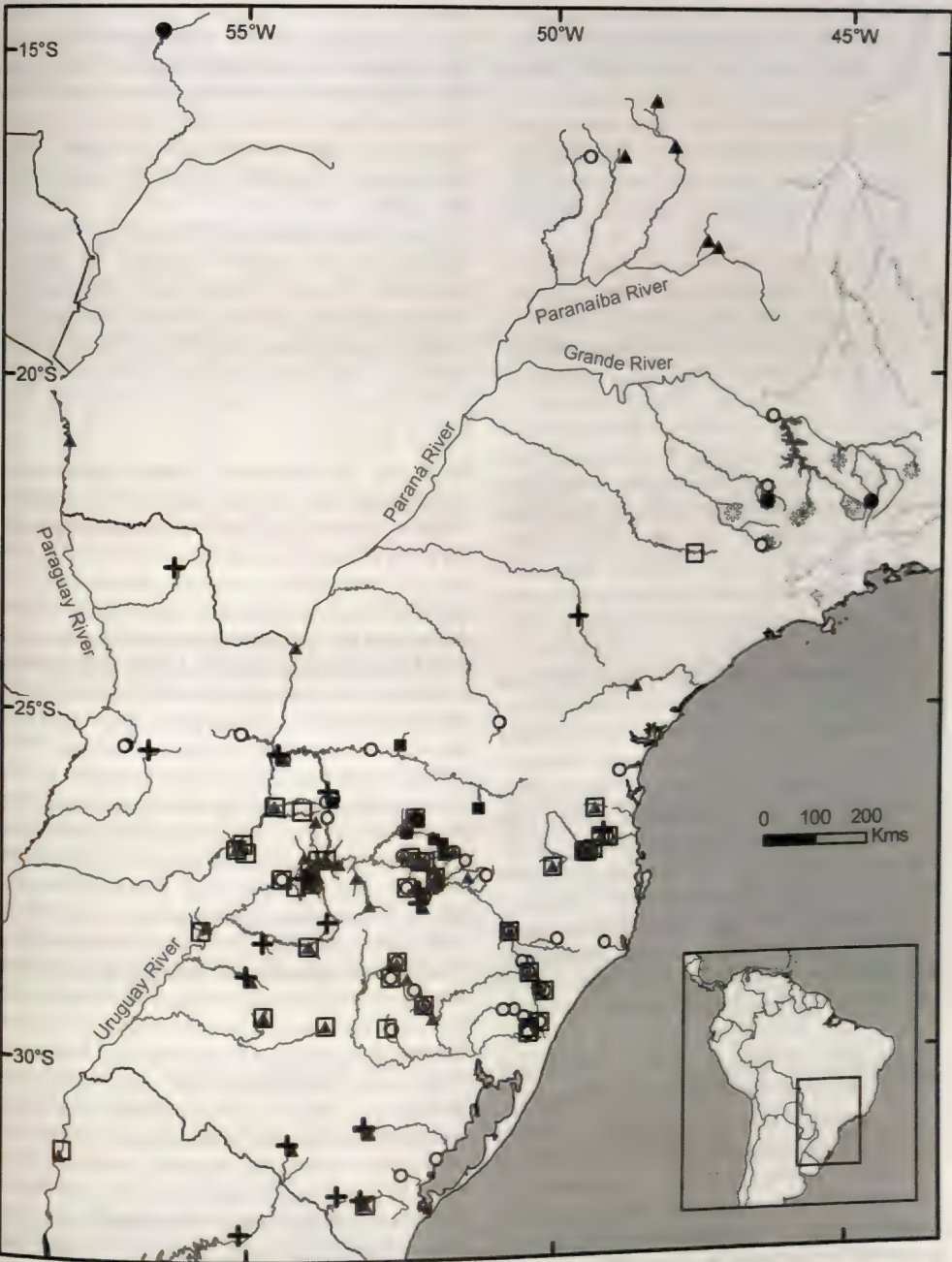


Figure 2. Distribution of eight species of Podostemaceae in the Paraná River System hydrographic region as demarcated by Ziesler and Ardizzone (1979). Representative large river names are included. Filled circle, *Castelnavia princeps*; plus sign, *Podostemum comatum*; open circle, *P. distichum*; filled square, *P. irgangii*; open square, *P. muelleri*; gray triangle, *P. ruifolium* subsp. *ruifolium*; filled triangle, *P. scaturiginum*; open asterisk, *P. weddellianum*.

Ten species occurred in the Eastern Brazil Area (Table 1, Fig. 3, Appendix 3), with six restricted to that region: *Ceratolacis pedunculatum*, *Cipoia ramosa*, *Diamantina lombardii*, *Lophogyne* sp. A, *Podostemum*

ovatum, and *P. saldanhanum*. *Diamantina lombardii* occurred in three river systems (one river in each), while *P. saldanhanum* occurred in two river systems and two rivers (four rivers total). Lastly, *Ceratolacis*

pedunculatum and *Cipoia ramosa* occurred only in the São Francisco River System; the former in four rivers and the latter in one. Four species in the eastern Brazil area were shared among other major areas or hydrographic basins (see below). Six species occurred in the São Francisco River System. The Doce and Paraíba do Sul river systems each had five species, with one to four species occurring in the remaining systems.

Five species were documented from more than one major area or hydrographic basin (*Castelnavia princeps*, *Cipoia inserta*, *Podostemum scaturiginum* (Mart.) C. T. Philbrick & Novelo, *P. weddellianum*, *Weddellina squamulosa*) (Table 1, Figs. 1–3, Appendix 3). *Podostemum weddellianum* (Table 1, Figs. 2, 3) occurred in the Eastern Brazil Area and Paraná River System. *Castelnavia princeps* and *P. scaturiginum* both occurred in the Amazon River System, while *Cipoia inserta* was documented from only the former two regions. Eastern Brazil Area, and Paraná River System. Only one species considered herein (*W. squamulosa*) occurred in the Guiana area and Orinoco River System regions, as well as the Amazon River System (Fig. 1).

Species that spanned more than a single major area or hydrographic basin did not exhibit equal distributions in the respective regions. For example, as many rivers in the Amazon River System had *Castelnavia princeps* as the Eastern Brazil Area and Paraná River System combined. Both *Podostemum scaturiginum* and *P. weddellianum* were most common in the Eastern Brazil Area, with *Weddellina squamulosa* being most common in the Amazon River System.

The number of species per river ranged from one to five (Appendix 3). Only a single species was documented from a majority (> 65%) of the ca. 200 rivers considered. Two rivers (Aripuanã, Teles Pires) in the Amazon River System had five species each. Several rivers in both the Amazon and Paraná hydrographic systems each had four species.

Current taxonomy: estimates of endemism. Thirteen of the 20 genera possessed at least a single one-river endemic species (Table 2). All species in three genera (*Macarenia*, 1 sp.; *Tulasneantha*, 1 sp.; *Wettsteiniola*, 3 spp.) were one-river endemics. For the other 17 genera, the percentage of one-river endemism ranged from 0% (*Diamantina*, *Lonchostephus*, *Lophogyne*, *Monostylis*, *Tristicha*, *Vanroyenella*, *Weddellina*) to 71% (*Oserya*). The two largest genera (*Apinagia*, *Rhyncholacis*) had 43% (22 spp.) and 32% (7 spp.) one-river endemism, respectively.

Podostemaceae occur in 22 Latin American countries, 10 of which have at least a single one-river endemic (Table 3). Brazil had the highest

number of one-river endemic species (26). Within Brazil, the number varied by state. Eight states had at least a single one-river endemic species; Pará (7) and Goiás (6) had the most. It remains unclear where three of the one-river endemics were collected in Brazil. Guyana had eight one-river endemic species, while three countries (Argentina, Colombia, Suriname) had three each.

Seven genera possessed at least one two-river endemic species (Table 2; *Apinagia*, *Jenmaniella*, *Marathrum*, *Mourera*, *Podostemum*, *Rhyncholacis*, *Vanroyenella*). The percentage of two-river endemism in these genera ranged from 9% in *Podostemum* to 100% in the monotypic *Vanroyenella*. The two largest genera (*Apinagia*, *Rhyncholacis*) had 41% (9 spp.) and 27% (6 spp.) two-river endemism, respectively.

IUCN Red List assessment. Species were placed preliminarily into one of five IUCN categories (Table 4, Appendix 2). Forty-one species, representing seven genera, were scored as Data Deficient (DD) (i.e., of questionable taxonomic status). Most DD species were in *Apinagia* (19), *Rhyncholacis* (8), and *Jenmaniella* (6). Forty-five species in 13 genera were scored as Least Concern (LC). Genera with the most LC species were *Apinagia* (13) and *Podostemum* (9). Of concern from a conservation perspective were species in the last three categories: Vulnerable (VU), Endangered (EN), and Critically Endangered (CR). Eleven genera contained species that were scored as VU D2 (with a restricted distribution), with the most in *Apinagia* (18) and *Rhyncholacis* (9). Species in five monotypic genera (*Diamantina*, *Lonchostephus*, *Macarenia*, *Tulasneantha*, *Vanroyenella*) were also VU.

Ten species in eight genera were scored as EN or CR (Table 4, Appendix 2). *Apinagia peruviana* and *Marathrum striatifolium* P. Royen were scored as CR by León (2006); we follow León's designations here. *Ceratolacis erythrolichen* (Tul. & Wedd.) Wedd. and *Podostemum flagelliforme* were assessed as CR because they have not been collected since their initial description in the 1800s, despite field studies in the region where they reportedly occurred (Philbrick & Bove, unpublished data). Two species of *Castelnavia* (*C. monandra*, *C. noveloi*) were documented each from a small region in a single river. *Lophogyne* sp. A was scored as EN B1ab(iii) by Bove et al. (in press), because its populations are scattered and it occurs in rivers heavily impacted by dam construction. The remaining two CR species are in *Wettsteiniola* (*W. accorsii* (Toledo) P. Royen, *W. apipensis*). Available evidence indicates that there have been extensive impacts from pollution and dam building, respectively, at the only known locations for these species. They are not scored as extinct because

efforts to locate them in their respective regions are as yet insufficient to make that determination.

Estimates of geographic range based on the IUCN (2009) EOO criteria illustrate considerable variation among species (Table 1). Of the 22 species scored, six were restricted to areas less than 100 km². Not surprisingly, these latter species occurred in only a few rivers. Species with increasingly broader areas also occurred. For example, one species had an EOO of about 6000 km², five species ranged from 20,000 to 100,000 km², and 10 species had > 200,000 km². The most widespread species had values in excess of 1,000,000 km² (*Castelnavia princeps*, *Podostemum distichum*, *Weddellina squamulosa*) (Table 1). Regression analyses indicated a significant relationship between EOO for a species and the number of rivers the species occurred in ($P < 0.05$). The relationship, however, was weak ($r^2 = 0.23$).

DISCUSSION

Endemism is a relative term that can be applied at various geographic scales in Neotropical Podostemaceae. For instance, all but two species (*Podostemum ceratophyllum* Michx., *Tristicha trifaria*) are endemic to the Neotropics. Species in South America, with the exception of *P. rutifolium* (cf. Philbrick & Novelo, 2004) and two species of *Marathrum*, are restricted to that continent. However, in our examination of endemism we focus on species with narrower geographic distributions. Our aim is to establish means for identifying which species are in need of conservation.

Taxonomic understanding is fundamental to interpreting the degree of species endemism in Podostemaceae. A goal of this study is to provide estimates that reflect current taxonomic understanding, realizing that in much of the family “current” does not mean adequate. Such genera as *Apinagia*, *Jenmaniella*, *Marathrum*, and *Rhyncholacis* remain in need of taxonomic study.

Clearly, the distribution of species of Podostemaceae throughout Neotropical countries is not uniform. Brazil, Guyana, and Suriname are especially rich in species (Table 3), while Central American countries have one to four species each. Not unexpectedly, one-river endemism is highest in the most species-rich countries, with Brazil (26 spp.) having the most.

We propose that a river, rather than a location where a given species occurs along a river, is the most applicable way to assess species distributions for Podostemaceae. Such a focus is also useful for understanding geographic patterns of species diversity, historical events that gave rise to that biodiversity, and human impacts that are detrimentally affecting it.

Table 3. The number of species and one-river endemics in each country. States are listed for Brazil.

Country	No. of species	No. of one-river endemic species (%)
Argentina	8	3 (37%)
Belize	1	0
Bolivia	4	1 (25%)
Brazil	58	26 (45%)
Amapá	3	2 (66%)
Amazonas	13	4 (31%)
Bahia	2	0
Ceará	1	0
Espírito Santo	4	0
Goiás	9	6 (67%)
Mato Grosso	8	0
Minas Gerais	14	3 (21%)
Pará	14	7 (50%)
Paraná	4	0
Piauí	1	0
Rio de Janeiro	6	0
Rio Grande do Sul	5	0
Rondônia	1	0
Roraima	12	1 (8%)
Santa Catarina	5	0
São Paulo	9	2 (22%)
Tocantins	10	3 (30%)
Unclear state	3	2 (66%)
Colombia	10	3 (30%)
Costa Rica	5	0
Cuba	1	0
Dominican Republic	1	0
Ecuador	1	0
El Salvador	1	0
French Guiana	8	0
Guatemala	2	0
Guyana	37	8 (22%)
Honduras	4	0
Mexico	6	1 (17%)
Nicaragua	2	0
Panama	2	0
Paraguay	4	1 (25%)
Peru	2	1 (100%)
Suriname	31	3 (10%)
Uruguay	3	0
Venezuela	28	2 (7%)

The latter issue—the nature of human impacts on tropical rivers—is particularly cogent when one considers the extent of one-river endemism in Neotropical members of the family.

Elements of both species biology of Podostemaceae, and the nature of human impacts on rivers, support our focus on rivers as conservation units. The unidirectional flow of water, combined with high seed set (cf. Philbrick & Novelo, 1997, 2004), support the prediction that plants throughout a river comprise a large meta-population. That is, sets of cataracts (or

Table 4. Summary of preliminary IUCN assessments for species in each genus recognized in current taxonomy. Total percent is based on the number of total species in the Neotropics (135).

Genus	Data Deficient (DD)	Least Concern (LC)	Vulnerable (VU D2)	Endangered (EN or CR)
<i>Apinagia</i>	19 (37%)	13 (27%)	18 (35%)	1 [Cr B1a,b(iii)] (2%)
<i>Castelnavia</i>	0	3 (60%)	0	2 (40%)
<i>Ceratolacis</i>	0	1 (50%)	0	1 [Cr B1b(iii)] (50%)
<i>Cipoia</i>	0	1 (50%)	0	1 (50%)
<i>Diamantina</i>	0	0	1 (100%)	0
<i>Jenmaniella</i>	6 (86%)	1 (14%)	0	0
<i>Lonchostephus</i>	0	0	1 (100%)	0
<i>Lophogyne</i>	0	0	0	1 [EN B1a,b(iii)] (100%)
<i>Macarenia</i>	0	0	1 (100%)	0
<i>Marathrum</i>	1 (10%)	5 (50%)	3 (30%)	1 [Cr B1a,b(iii)] (10%)
<i>Monostylis</i>	0	1 (100%)	0	0
<i>Mourera</i>	2 (33%)	2 (33%)	2 (33%)	0
<i>Oserya</i>	4 (57%)	2 (29%)	1 (14%)	0
<i>Podostemum</i>	0	9 (82%)	1 (9%)	1 [Cr B1b(iii)] (9%)
<i>Rhyncholacis</i>	8 (36%)	5 (23%)	9 (41%)	0
<i>Tristicha</i>	0	1 (100%)	0	0
<i>Tulasmeantha</i>	0	0	1 (100%)	0
<i>Vanroyenella</i>	0	0	1 (100%)	0
<i>Weddellina</i>	0	1 (100%)	0	0
<i>Wettsteiniola</i>	1 (33%)	0	0	2 [Cr B1b(iii)] (67%)
Total	41 (30%)	45 (33%)	39 (29%)	10 (7%)

waterfalls) separated by expanses of quiet water support populations that interact genetically via seed dispersal. Large dams have the most pervasive detrimental impacts on species of Podostemaceae in the Neotropics. Both the reservoir upstream of a dam and the long reaches of rivers downstream that experience manipulated water levels are detrimental to populations.

ONE- AND TWO-RIVER ENDEMISM

Comparison of the current taxonomy with that of Royen (1951, 1953, 1954) indicated a reduction in the estimated number of one-river endemics from 48% to 37%. In a general sense, such change is not surprising as the latter reflects five decades of additional study. *Castelnavia* and *Podostemum*, for instance, have recently been monographed (Philbrick & Novelo, 2004; Philbrick et al., 2009). In both, the proportion of one-river endemics has been reduced. Reduction in the number of recognized species of *Marathrum* by almost 50% is also notable (Novelo et al., 2009) in that the number of one-river endemics was reduced by only one. The taxonomy of much of Podostemaceae remains problematic (cf. Philbrick & Novelo, 1995; Berry, 2004). Future studies will no doubt result in modification of estimates provided here.

It is remarkable that of the 50 species (37% of the family in the Americas) currently interpreted as one-

river endemics, 35 (70%) are DD; their taxonomic status is uncertain and including them in estimates may be misleading. Indeed, incomplete understanding of the taxonomy and geographic distribution of species hinders accurate estimates of endemism. Consequently, we present two estimates. If upon further analyses all DD species remain recognized as taxonomically valid, then the 37% estimate of one-river endemism is meaningful. Conversely, if further analyses of DD species lead to all of them being reduced to synonymy, then the percentage of one-river endemism would be reduced to 15%. As a result, our best estimate of one-river endemism in Neotropical Podostemaceae is between 15% and 37%.

It is notable that 22 species (current taxonomy) are two-river endemics and about one third of them are DD. If all DD one- and two-river endemic species are supported as valid by further study, more than half of the family (54%) would be included. By contrast, if all DD one- and two-river endemic species (42 spp. total) are shown to be synonymous with other species, then 33% of the family would be one- or two-river endemics. Even if the latter is the case, one third is a significant proportion. A key issue, of course, is whether the presently documented species distributions are accurate representations of actual distributions. Results of ongoing field studies by the first two authors (Philbrick, Bove) support the prediction that for many species, they are not.

Perhaps not surprisingly, the incidence of one-river (18.2%) and two-river (9.1%) endemism was markedly lower for the 22 species included in the river-by-river component of this study (see below) than for estimates based on Royen (1951, 1953, 1954) and current taxonomy. Many of these representative species were in genera that have recently been monographed. Consequently, their geographic ranges are more thoroughly documented.

Reports in the early literature (e.g., Willis, 1902) indicated that some species only exist at one small area in a river, e.g., a single waterfall or single set of river rapids. The whole-river approach utilized here does not allow us to test this idea, *per se*. It should be pointed out, however, that during field studies throughout Mexico and Central and South America over 15 years, only a single species (*Castelnavia noveloi*) occurred at one "location." *Castelnavia noveloi* is presently known from only a 0.5–1-km region of the Taquaruçu River, Tocantins, Brazil. Whether the species has a broader distribution in that river remains to be determined.

MEASURES OF GEOGRAPHIC RANGE AND SPECIES ENDEMISM

Geographic ranges for many Neotropical Podostemaceae remain poorly documented. Representative species studied with GIS, most of which represent taxa from south of the Amazon River, illustrate a diversity of geographic ranges. For these species we propose two regional categories for discussion. "Narrow" regional species are those with a range of ≤ 500 km along the longest geographic axis of their distribution, while the longest axis for "broad" regional species is 750–1500 km. These categories, although arbitrary, provide meaningful reference points for discussion as they encompass presently documented species ranges.

Eight species, representing five genera, have narrow regional distributions in south-central Brazil. One species of *Cipoia* (*C. ramosa*), the single species of *Diamantina*, and one of two species of *Ceratolaxis* (*C. pedunculatum*) occur only in central and southeastern Minas Gerais, i.e., the Eastern Brazil Area (Fig. 3). The single species of *Lophogyne* (*Lophogyne* sp. A) is restricted largely to the state of Rio de Janeiro (Bove et al., in press; Fig. 3). *Podostemum* occurs in North, Central, and South America, yet the majority (eight of 11) of the species are restricted to the Paraná River System hydrographic region and Eastern Brazil Area (Figs. 2, 3; cf. Philbrick & Novelo, 2004). *Podostemum flagelliforme* is documented from a single location in Tocantins (Fig. 1). *Podostemum irgangii*, *P. ovatum*, and *P. saldanhanum* all occur in several locations but have narrow geographic ranges (Figs. 1–3; cf. Philbrick & Novelo,

2004). The former occurs in a small region in the states of Santa Catarina and adjacent Paraná. *Podostemum ovatum* ranges from eastern São Paulo State, northeast through Rio de Janeiro to Espírito Santo. Lastly, *P. saldanhanum* is documented only from a small region in the state of Rio de Janeiro.

Among species in Mexico, where species distributions are well known (cf. Novelo & Philbrick, 1997), there is only one narrow regional species (the one-river endemic *Oserya longifolia*). Although *Podostemum rutifolium* subsp. *ricciiforme* (Liebm.) Novelo & C. T. Philbrick has a narrow distribution in Mexico, the subspecies is also reported from western Colombia (see fig. 26 in Philbrick & Novelo, 2004). A historic collection documents it for Costa Rica, but during recent fieldwork there it could not be relocated (G. E. Crow, pers. comm.).

Many species have broad regional distributions. Species representing nine genera are presented as examples. Two occur in Mexico (*Oserya coulteriana*, *Vanroyenella plumosa*), both on the western slope of the country. The former also is documented from Baja California Sur (Novelo & Philbrick, 1997). *Apinagia nana* and *O. perpusilla* range from central Venezuela to southwestern Suriname (Werkhoven & Peeters, 1993; Appendix 1). The other examples occur primarily in Brazil. *Cipoia inserta* spans from southeastern Minas Gerais northwest to eastern Goiás. *Monostylis capillacea*, *Lonchostephus elegans*, and *Tulasneantha monadelpha* (Bong.) P. Royen span from northern Pará to western Mato Grosso. The former is also documented from eastern Bolivia. *Castelnavia fluitans* ranges from northern Tocantins to western Mato Grosso (Fig. 1). Five species (and one subspecies) of *Podostemum* are also broadly regional. *Podostemum comatum*, *P. distichum*, *P. muelleri*, and *P. rutifolium* subsp. *rutifolium* have overlapping ranges in southern Brazil and northeastern Argentina (Fig. 2). *Podostemum scaturiginum* and *P. weddellianum* occur north of the previously mentioned four taxa. The former spans from Espírito Santo west to Goiás, while the latter is common in Minas Gerais and Rio de Janeiro (Fig. 2). Moreover, Kelloff and Funk (2004) noted that seven species of *Jenmaniella* and *Rhyncholaxis* are endemic to the Guiana Shield.

Some species have distributions larger than 1500 km. Although a detailed account is beyond the scope of this paper, a few species are illustrative. The two most widespread species in the Americas are *Tristicha trifaria* and *Podostemum ceratophyllum*. The former is essentially pantropical and occurs throughout the entire distribution of the family in Central and South America (Mexico to Argentina) and also in the Old World (e.g., Royen, 1951). The largely temperate *P. ceratophyllum* ranges across eastern North America

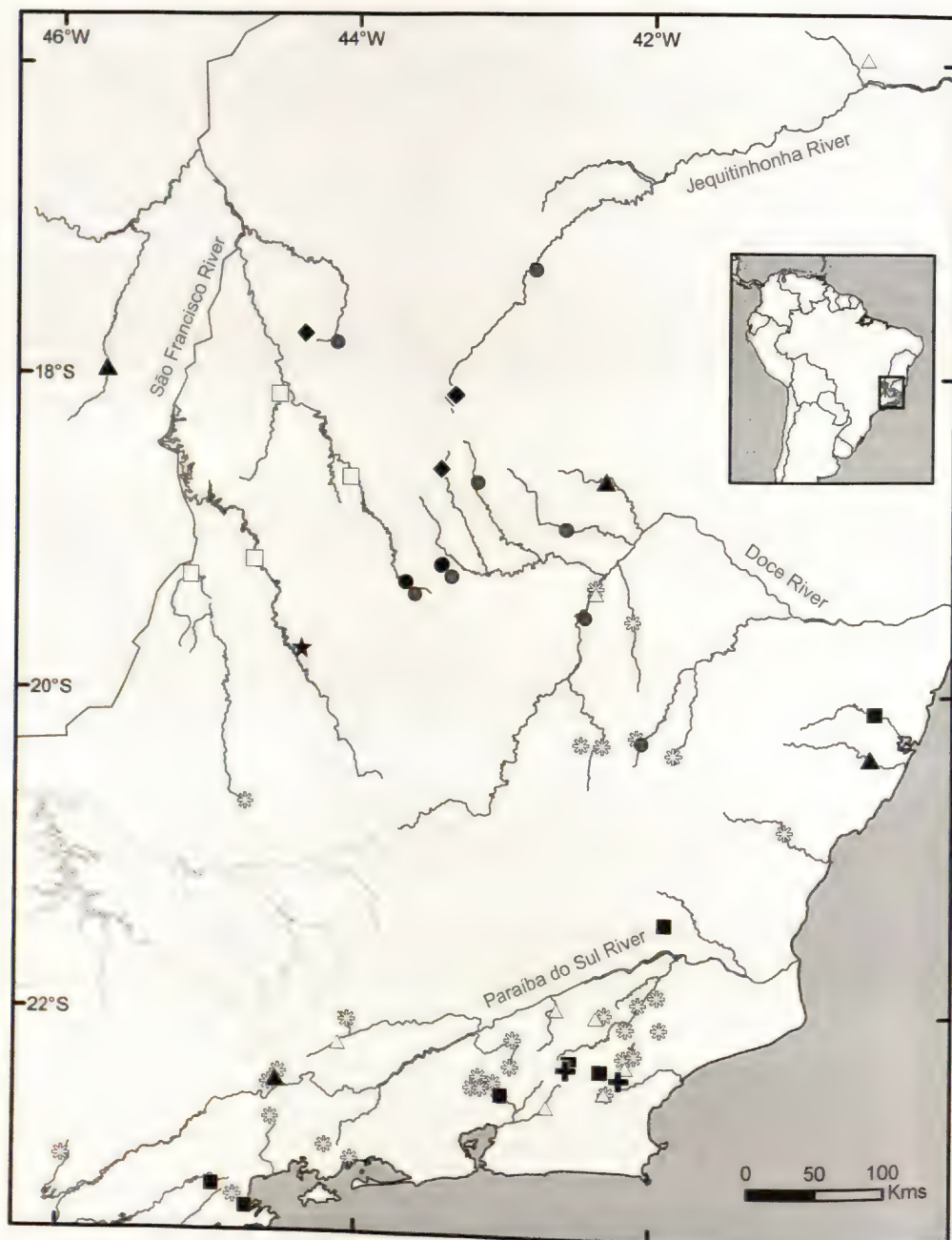


Figure 3. Distribution of 10 species of Podostemaceae in the eastern Brazil area, as demarcated by Ziesler and Ardizzone (1979). Representative large river names are included. Filled circle, *Castelnavia princeps*; open square, *Ceratolacis pedunculatum*; gray circle, *Cipoia inserta*; star, *Cipoia ramosa*; diamond, *Diamantina lombardii*; open triangle, *Lophogyne* sp. A; filled square, *Podostemum ovatum*; plus sign, *P. saldanhanum*; filled triangle, *P. scaturiginum*; open asterisk, *P. weddellianum*.

north to New Brunswick and Nova Scotia, Canada, with disjunct populations in Honduras and the Dominican Republic (Philbrick & Novelo, 2004). *Weddellina squamulosa* exhibits a wide distribution across Venezuela, the Guianas, and northern and central Brazil (Fig. 1). *Mourera fluviatilis* Aubl., the most easily recognized member of the family, is broadly distributed across northern South America (Venezuela, Guyana, Suriname, French Guiana, northern Brazil). Several species of *Apinagia* (e.g., *A. longifolia*, *A. richardiana*) also show a broad distribution across northern South America.

Estimates of EOO (IUCN, 2009) also demonstrated a diversity of geographic ranges among species. Not surprisingly, species with the lowest EOO values (i.e., < 100 km²) also occurred in the smallest number of rivers (one or two). Overall, however, EOO was shown to be a poor predictor of the number of rivers a species was documented from. As is true for other riverine species, EOO has notable limitations as a measure of geographic range of species of Podostemaceae. Such geographic estimates cannot account for the extent of appropriate habitat (i.e., river rapids and waterfalls) within an identified geographic range or selected river.

Assessment of the number of rivers that a given species occupies is informative, but this measure is also limited in its value. A more useful measure of species range is one that integrates the extent of appropriate habitat within a river. Such a measure has not yet been developed for Podostemaceae.

MAIN AREAS, HYDROGRAPHIC BASINS, RIVER SYSTEMS, AND RIVERS

Consideration of species distributions within hydrographic regions, major areas, river systems, and rivers, although limited in taxonomic scope (22 species), was revealing. All three main focal areas or hydrographic basins (Amazon River System, Eastern Brazil Area, Paraná River System) were similar in the number of species they contained (eight to 10), yet each had unique elements of its podostemad flora. For example, the monotypic genus *Monostylis* occurred only in the Amazon River System, as did most species of *Castelnavia*. In the Eastern Brazil Area were species of *Ceratolacis* and *Diamantina*, which did not occur elsewhere. Although no genera were restricted to the Paraná River System, five species of *Podostemum* were. None of the three primary main areas or hydrographic basins possessed a completely unique podostemad flora. Conversely, some species of *Castelnavia*, *Cipoia*, and *Podostemum* spanned hydrographic regions. In some instances, a majority of a species distribution occurred in one main area or hydrographic basin, with a limited distribution in another.

Within hydrographic regions certain river systems and rivers harboured more species than others. In the Amazon River System basin, three of the seven river systems contained six or more species; the Tocantins River System contained 10. The Eastern Brazil Area and Paraná River System also varied, with the number of species per river system ranging from one to six. Detailed analyses of broader taxonomic samples that consider how species diversity is related to drainage basin, river length, and other elements of river systems (e.g., geology, extent of appropriate habitat, latitude) are needed.

Werkhoven and Peeters (1993), in their consideration of Podostemaceae in Suriname, were the first to take a river-by-river approach to assessing species distributions. Such an approach herein revealed several patterns. First, a majority (> 65%) of rivers in all hydrographic regions and main areas contained only a single species. Yet, notable numbers of rivers contained more than one. The number of rivers with more than a single species ranged from 15 (24%) in the eastern Brazil area, to 35 (34%) and 12 (39%) in the Paraná and Amazon river systems, respectively. Clearly all rivers are not equal in species diversity. It is also apparent that in large river systems, more species occur in tributaries than in the main channel. Perhaps this is not surprising, as tributaries comprise proportionally more river system length than main channels.

IMPACTS ON PODOSTEMACEAE

Rivers are heavily impacted tropical aquatic habitats (e.g., Sioli, 1986; Dudgeon et al., 2006). Habitat destruction is the single most important threat to river biota (Giller & Malmqvist, 2002). Siltation, pollution (domestic, industrial, agricultural), and water flow manipulation all influence ecological patterns in tropical rivers. The damming of large rivers is an especially important factor that reduces river biodiversity (Young-Seuk et al., 2003). The presence of large dams (e.g., hydropower, flood control, water supply functions) results in major changes to riverine biota (e.g., Petts, 1984; Bonetto et al., 1989; Allan, 1996; Nilsson & Berggren, 2000; Pringle et al., 2000; Odinetz-Collart et al., 2001; Poff et al., 2007). Pringle et al. (2000) discussed the impact of large hydropower dams on freshwater fish and mollusks. Many issues discussed in Pringle et al. are equally applicable to Podostemaceae.

Five ecological conditions are central to persistence of populations of Podostemaceae (Philbrick & Novelo, 2004): seasonal water level change (crucial for sexual reproduction and seed dispersal), solid substratum, swift clean water (at least seasonally), high light intensity, and a biofilm of bacteria. Field observations

Table 5. Examples of large dams in Argentina, Brazil, Paraguay, Suriname, Uruguay, and Venezuela. For each, the river name, dam name, and estimated reservoir length upstream of dam are indicated.

Country	River	Dam name	Estimated reservoir length (km)
Brazil	Tocantins	UHE Lageado-Palmas	110
Brazil	Tocantins	Serra da Mesa	130
Brazil	Araguaia	Tucuruí	110
Brazil	Paraná	Itaipu	140
Brazil	Tietê	Três Irmãos	150
Brazil	Paranapanema	Jurumirim	70
Brazil	Uruguai	Itá	71
Brazil	Uruguai	Machadinho	40
Brazil	Grande	Água Vermelha	95
Brazil	Grande	Marimbondo	80
Brazil	Grande	Porto Colômbia	40
Brazil	Grande	Volta Grande	60
Brazil	Grande	[unclear]	61
Brazil	Grande	Jaguara II	25
Brazil	Grande	Estreito	26
Brazil	Grande	Mascarenhas de Moraes	75
Brazil	Grande	Furnas	100
Brazil	São Francisco	Sobradinho	320
Suriname	Suriname	Afobaka	65
Venezuela	Caroní	Guri	125
Argentina-Uruguay	Uruguay	Salto Grande	90
Argentina-Paraguay	Paraná	Yacyretá	100

indicated that altering natural fluctuations in water levels disrupts sexual reproduction, and consequently recruitment via seed, which is fundamental to maintaining populations.

Obviously, dams have a dramatic influence on water flow. Upstream of a dam the lotic hydrologic regime is changed into a lentic regime; a river becomes a reservoir. Inundation of river rapids and waterfalls by reservoirs makes them inhospitable to Podostemaceae. Such reservoirs can extend many kilometers upstream. Table 5 lists representative large dams in Argentina, Brazil, and Venezuela that occur within regions rich in Podostemaceae. In these examples, reservoirs from individual dams extend 25 km to > 300 km upstream. Many rivers have multiple dams. For example, three are constructed along the Tocantins River, with a combined reservoir length of about 280 km. The Grande River, which forms much of the boundary between the Brazilian states of Minas Gerais and São Paulo, has nine dams, with a combined reservoir length of more than 550 km. Multiple large dams are also present on several tributaries of the Paraná River (Bonetto et al., 1989).

Large dams influence the occurrence of aquatic biota downstream as well, due to hydrologic and geomorphic effects (Graf, 2006). For example, patterns of siltation, erosion, and timing of peak floods and their durations are all influenced by large dams

(e.g., Ward, 1982; Petts, 1984; Pringle et al., 2000). Poff et al. (1997) emphasized the importance of the timing of high/low water levels to river biota. Management of water release from dams results in temporal changes to flooding patterns relative to natural water flow, and thus impacts river biota. Nilsson and Berggren (2000) discussed how riparian communities are influenced downstream of dams, and Kingsolving and Bain (1993) showed that fish abundance and diversity were diminished. It is remarkable that water released from a major reservoir in Suriname remained low in oxygen for more than 100 km downstream (van der Heide, 1976). Change in water chemistry could have profound effects on populations of Podostemaceae, which have been shown to be negatively influenced, or lost altogether, downstream of large dams (Jégu & dos Santos, 1987; Odinetz-Collart et al., 2001). We predict that negative effects downstream of dams will extend as far as managed water level manipulations persist. Consequently, a large dam can have negative impacts on Podostemaceae populations for considerable distances both upstream and downstream.

Anecdotal accounts indicate that large dams have resulted in the loss of populations of Podostemaceae. Dam construction was evidently a central factor in the apparent extinction of *Wettsteiniola apipensis* in the Paraná River, Argentina (Tur, 1997). In Peru, one of

few locations for *Apinagia peruviana* is now covered by a hydroelectric dam (B. León, pers. comm.). Some of the locations in which ecological studies were conducted by Grubert (e.g., 1975, 1976) in the Caroni River (Venezuela) are now beneath the reservoir of the Guri Dam. The only known location where *Podostemum flagelliforme* (Philbrick & Novelo, 2004) was documented is now covered by the reservoir associated with the Lajeado Dam (Tocantins River, Tocantins, Brazil). *Apinagia guairaensis* Fiebrig and *Wettsteiniola pinnata* Suess. could well be extinct as a consequence of the submergence of the Sete Quedas waterfalls when the Itaipu hydroelectric dam was constructed in the Paraná River. In addition, the only known Brazilian population of *Apinagia yguazuensis* Chodat & Vischer has been lost from the Itaipu location. We predict that populations of many other species of Podostemaceae have been extirpated because of dam construction even though relatively few have yet been documented.

Podostemaceae are restricted to habitats that are heavily impacted by human activities. Our preliminary assessments of species of Podostemaceae using the IUCN categories are revealing. About one third of the species can be confidently assessed as being LC, i.e., occurring in enough rivers such that there is little current danger of extinction. The remaining two thirds are either DD, VU, EN, or CR.

Taxonomic study is central to establishment of reliable estimates of species endemism and clarification of which species are in need of conservation. Many of the species presently recognized, and scored as DD, are based on single and/or incomplete collections. Such paucity of specimens hinders the ability to understand patterns of variation in this family of plants distinguished by remarkable vegetative plasticity. Understanding patterns of variation is key to establishing reliable taxonomies, and taxonomic understanding remains unreliable for about one third of the species in the Neotropics.

Increasing demand for hydropower has the potential to result in major negative impacts on Podostemaceae. The Report of the World Commission on Dams (2000) estimated that > 90% of power generated in Brazil is from hydroelectric sources. Indeed, reliance on hydropower in Brazil is projected to increase in the future. Pringle et al. (2000) reported that 70 dams are planned for the Amazonian region of Brazil alone, while the Report of the World Commission on Dams (2000) listed 140 "new hydro investments" for the next decade. The degree of current and future dam construction is a key issue relating to conservation of Podostemaceae in Latin America, especially Brazil. Understanding the distribution of species in river systems and rivers provides a means of predicting

where new large dam construction will have the most detrimental impacts. Such insight is important for establishing which species are in need of conservation.

CONCLUSIONS

The present study provides an assessment of species distributions in Neotropical Podostemaceae, with a focus on those that have the smallest geographic ranges. Species in the family exhibit a range of geographic distributions. Some are widespread, while others display progressively smaller ranges. One-river endemic species account for 15%–37% of the family. Further refinements of these estimates will only be possible after understanding of the taxonomy and distribution of species is enhanced. The percentage of one-river endemic species that are poorly known taxonomically is remarkable (70%). Understanding of the distributions of species whereby the number of river systems and rivers is taken into account provides more meaningful insight for Podostemaceae than measures based solely on overall geographic range.

Systematic studies enhance understanding of the nature of species and their geographic distributions. Not surprisingly, genera in which species distributions are best documented are those that have been recently monographed. In each, the number of one-river endemics was reduced.

Humans continue to have major impacts on tropical rivers; Podostemaceae rely on the natural flow of these rivers for their survival. Large dams disrupt the natural flow of rivers and thus negatively impact populations of Podostemaceae. Increasing pressures to tap the vast hydropower potential in South America will have negative consequences on the diversity of Podostemaceae on the continent.

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APPENDIX 1. Representative voucher specimens for previously undocumented locations of *Apinagia boliviiana*, *A. fimbriifolia*, *A. nana*, *A. peruviana*, *Cipicia inserta*, *Diamantina lombardii*, *Lonchostephus elegans*, *Marathrum utile*, *Monostylis capillacea*, *Oserya perpusilla*, and *Weddellina squamulosa* in Ecuador, Bolivia, Brazil, Honduras, Suriname, and Venezuela.

Apinagia boliviiana P. Royen. BOLIVIA. **La Paz:** Nor Yungas, Huarinilla River, 18 May 1996. *Ritter* 3198 (NHA); Idem, Corico River, 18 May 1996. *Ritter* 3196 (NHA).

Apinagia fimbriifolia P. Royen. BRAZIL. **Torantim:** Balsas River, 11°14'S, 47°29'06"W, 27 July 2006. *Philbrick et al.* 6004 (R, WCSU); Novo River, 10°15'39"S, 46°53'2"W, 15 June 2010, *Bove et al.* 2234 (R, WCSU).

Apinagia nana Went. SURINAME. **Sipaliwini:** Bufuhulu, Suriname River, 4°01'27.7"N, 55°28'4.6"W, 27 Oct. 2007. *Philbrick et al.* 6211 (BBS, WCSU); Jaba-Kondre, Suriname River, 4°5'16.2"N, 55°27'9.4"W, 27 Oct. 2007. *Philbrick et al.* 6215 (BBS, WCSU); Gunsee, Suriname River, 4°22'53.1"N, 55°23'23.4"W, 30 Oct. 2007. *Philbrick et al.* 6232 (BBS, WCSU); Drietaabietie, Tapanahoni River, 4°0'34.4"N, 54°48'36.1"W, 1 Nov. 2007. *Philbrick et al.* 6237 (BBS, WCSU); Maroni (Marowijne) River, 4°28'43.3"N, 54°26'12.9"W, 4 Nov. 2007. *Philbrick et al.* 6258 (BBS, WCSU). VENEZUELA. **Bolívar:** Sucre, Caura River, Surapire Raudal, 6°28'5.5"N, 64°45'59.5"W, 9 Jan. 2007. *Philbrick & Lasso* 6022 (CAR, WCSU).

Apinagia peruviana (Wedd.) Engl. ECUADOR. **Azuay:** Patu River, 28 May 1943. *Steyermark* 52759 (NY).

Cipoia inserta C. T. Philbrick, Novelo & Irgang. BRAZIL. **Goiás:** Alto Paraíso de Goiás, Coudros River, 14°9'38"S, 47°35'39"W, 11 June 2010, Bove et al. 2205 (R, WCSU); Alto Paraíso de Goiás, Preto River, 14°9'28"S, 47°50'10"W, 11 June 2010, Bove et al. 2208 (R, WCSU); Alto Paraíso de Goiás, Cobras River, 14°9'42"S, 47°37'50"W, 12 June 2010, Bove et al. 2212 (R, WCSU); Teresina de Goiás, Almas River, 13°46'42"S, 47°25'22"W, 13 June 2010, Bove et al. 2222 (R, WCSU).

Diamantina lombardii Novelo, C. T. Philbrick & Irgang. BRAZIL. **Minas Gerais:** Lassance, Corrente River, 17°44'4"S, 44°21'56"W, 21 June 2010, Bove et al. 2253 (R, WCSU).

Lonchostephus elegans Tul. BRAZIL. **Mato Grosso:** Colniza (Panelas), Roosevelt River, 9°9'52.1"S, 60°44'11"W, 25 Sep. 2007, Bove & Philbrick 1899 (R, WCSU). **Tocantins:** São João do Araguaia, Araguaia River, 5°18'28.5"S, 48°55'34.2"W, 22 July 2006, Philbrick et al. 5976 (R, WCSU).

Marathrum utile Tul. HONDURAS. **Atlántida:** Jimamito Nuevo, Jilamito, 15°30'N, 87°34'W, 3 Nov. 1996, Maas & Mass 8495 (EAP).

Monostylis capillacea Tul. BOLIVIA. **Santa Cruz:** Velasco, Itenez River, 13°39'8"S, 60°48'47"W, 29 June 1998, Ritter et al. 4410, 4411, 4413 (NHA, WCSU). BRAZIL. **Mato Grosso:** Apiacás, Apiacás River, Cachoeira dos Papagaio, 9°19'11.9"S, 57°4'18.8"W, 21 Sep. 2007, Bove & Philbrick 1878 (R, WCSU); Apiacás, Apiacás River, 9°17'59.4"S, 57°4'5.2"W, 21 Sep. 2007, Bove & Philbrick 1883 (R, WCSU); Humboldt, Aripuanã River, 6 Oct. 1973, Berg & Steward P18570 (U); Aripuanã, Aripuanã River, Cachoeira dos Dardanelos, 10°9'50.9"S, 56°27'12.8"W, 23 Sep. 2007, Bove & Philbrick 1898 (R, WCSU); Juruena River, Cachoeira Salto Augusto, 28 May 1977, Rosa & Santos 2030 (RB); Colniza (Panelas), Roosevelt River, 9°9'49.2"S, 60°44'25.8"W, 25 Sep. 2007, Bove & Philbrick 1906 (R, WCSU); Alta Floresta, Teles Pires River, Porto de Areia, 9°38'22.2"S, 55°59'43.3"W, 16 Sep. 2007, Bove & Philbrick 1852 (R, WCSU). **Pará:** Cachoeira Bobiré, Tapajós River, 29 July 1923, Ducke s.n. (RB). **Rondônia:** Cachoeira de Sta. Cruz, Jamari River, 28 June 1965, Pires & Martin 9974 (NY). **Tocantins:** Lajeado, Lajeado River, 9°50'9"S, 48°17'38"W, 7 July 2005, Philbrick et al. 5825 (MEXU, R, WCSU); Taquaruçu, Taquaruçu River, 10°18'21"S, 48°10'18"W, 6 Aug. 2005, Philbrick et al. 5832 (MEXU, R, WCSU).

Oserya perpusilla (Went) P. Royen. SURINAME. **Sipaliwini:** Amotopo, Lucie River, 3°34'49"N, 57°39'0"W, 21 Oct. 2007, Philbrick et al. 6189 (BBS, WCSU); Bufuhulu, Suriname River, 4°1'27.7"N, 55°28'4.6"W, 27 Oct. 2007, Philbrick et al. 6212 (BBS, WCSU); Drietabbetie, Tapanahoni River, 4°1'52"N, 54°47'57.7"W, 1 Nov. 2007, Philbrick et al. 6240 (BBS, WCSU); Jaba-Kondre, Suriname River, 4°5'16.2"S, 55°27'9.4"W, 27 Oct. 2007, Philbrick et al. 6216 (BBS, WCSU); Keyserberg, Zuid River, 3°4'6.7"N, 56°29'1.2"W, 15 Oct. 2007, Philbrick et al. 6145 (BBS, WCSU); Poelgoedoe, Lawa River, 4°19'23.5"N, 4°23'31.9"W, 3 Nov. 2007, Philbrick et al. 6254 (BBS, WCSU). VENEZUELA. **Bolívar:** Sucre, Caura River, 6°53'59.7"N, 64°50'7.2"W, 9 Jan. 2007, Lasso et al. 6014 (CAR, WCSU); Idem, Nichare River, 6°32'8.1"N, 64°49'48.9"W, 12 Jan. 2007, Lasso et al. 6040 (CAR, WCSU); Sifontes, Paragua River, Uraima Falls, 6°18'7.3"N, 63°37'22.6"W, 14 Jan. 2007, Lasso et al. 6047 (CAR, WCSU).

Weddellina squamulosa Tul. BRAZIL. **Goiás:** 60 km NW of Portelândia, Matrinchã River, 16°58'11"S, 52°37'15"W, 18 May 2000, Philbrick et al. 5587 (ICN, MEXU, WCSU); Caiapônia, waterfall of Bonito River, 16°48'51"S, 51°42'11"W, 20 May 2000, Philbrick et al. 5599 (ICN, MEXU, WCSU); Idem, Ribeirão Monte, 16°57'7"S, 51°50'0"W, 20 May 2000, Philbrick et al. 5600 (ICN, MEXU, WCSU). **Mato Grosso:** Apiacás, Apiacás River, Cachoeira dos Papagaio, 9°19'11.9"S, 57°4'18.8"W, 21 Sep. 2007, Bove & Philbrick 1879 (R, WCSU); Aripuanã, Aripuanã River, 10°9'50.9"S, 59°27'12.8"W, 23 Sep. 2007, Bove & Philbrick 1895 (R, WCSU); Bandeirante, Juruena River, 9°57'2.3"S, 56°13'45.7"W, 22 Sep. 2007, Bove & Philbrick 1889 (R, WCSU); Colniza (Panelas), Roosevelt River, 9°9'52.1"S, 60°44'11"W, 25 Sep. 2007, Bove & Philbrick 1902 (R, WCSU); Paranaita, Teles Peres River, 9°14'33.6"S, 56°50'31.7"W, 19 Sep. 2007, Bove & Philbrick 1876 (R, WCSU); 29 km from Torixoréu, Peixe River, 16°18'25"S, 52°44' 43"W, 18 May 2000, Philbrick et al. 5580 (ICN, MEXU, WCSU). **Pará:** Jacareacanga, São Benedito River, 9°3'11.5"S, 56°35'7.3"W, 18 Sep. 2007, Bove & Philbrick 1862 (R, WCSU). **Rondônia:** Pacaás River, 27 Mar. 1978, Santos et al. 280 (RB); Porto Velho, 18 Aug. 1963, Maguire 56718 (VEN). **Tocantins:** Lajeado, Lajeado River, 9°50'9"S, 48°17'38"W, 7 July 2005, Philbrick et al. 5822 (MEXU, R, WCSU).

APPENDIX 2. Species recognized by Royen (1951, 1953, 1954) and current taxonomy, country in which each occurs, number of rivers in which each was reported by Royen, and the current taxonomy, IUCN determination for each species, and source of information provided subsequent to Royen. Cook and Rutishauser (2001) transferred species of *Mniopsis* to *Crenias*. For brevity, these nomenclatural changes are not shown here.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>Apinagia arminensis</i> P. Royen	Su., Fr. Gu.	2	2	VU	
<i>A. batrachifolia</i> (Mildbr.) P. Royen*	Br.	1	(3)	VU	
<i>A. boliviana</i> P. Royen	Bo.	(2)	(3)	VU	Appendix 1
<i>A. brevicaulis</i> Mildbr.	Ve.	1	1	VU	Berry (2004)
<i>A. corymbosa</i> (Tul.) Engl.*	Br., Co., Guy., Su., Ve.	5	(7)	LC	Berry (2004)
<i>A. crispa</i> P. Royen	Su.	1	1	DD	

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>A. digitata</i> P. Royen	Fr. Gu., Su.	(2)	2	VU	Werkhoven & Peeters (1993)
<i>A. divaricata</i> Tul. & Wedd.	Br.	1	1	DD	
<i>A. divertens</i> Went ex Pulle	Guy., Su.	1	4	LC	Schnell (1969), Werkhoven & Peeters (1993)
<i>A. exilis</i> (Tul.) P. Royen	Guy., Su., Ve.	2	3	VU	Berry (2004)
<i>A. fimbriifolia</i> P. Royen	Br.	1	2	VU	
<i>A. flexuosa</i> (Tul.) P. Royen	Fr. Gu., Su.	(2)	4	LC	Schnell (1969), Werkhoven & Peeters (1993)
<i>A. fluitans</i> P. Royen	Bo.	1	1	DD	
<i>A. fucoides</i> Tul.	Br.	4	4	LC	
<i>A. glaziovii</i> (Warm.) P. Royen	Br.	1	1	DD	
<i>A. goejei</i> Went ex Pulle	Su.	2	2	VU	
<i>A. guairensis</i> Fiebrig	Par.	1	1	DD	
<i>A. guyanensis</i> (Pulle) P. Royen	Fr. Gu., Su., Ve.	(6)	> 15	LC	
<i>A. hulkiana</i> (Went) P. Royen	Guy., Su.	2	2	VU	Werkhoven & Peeters (1993)
<i>A. inthurnii</i> (K. I. Goebel) P. Royen	Guy., Su.	1	2	VU	Werkhoven & Peeters (1993)
<i>A. itanensis</i> Schnell	Guy.	n.a.	1	VU	Schnell (1969)
<i>A. kochii</i> (Engl.) P. Royen	Br., Fr. Gu., Ve.	1	> 15	LC	Philbrick (2002), Berry (2004)
<i>A. latifolia</i> (K. I. Goebel) P. Royen	Guy.	1	1	DD	
<i>A. leptophylla</i> (K. I. Goebel) P. Royen	Guy.	1	1	DD	
<i>A. longifolia</i> (Tul.) P. Royen	Fr. Gu., Guy., Su., Ve.	(5)	> 15	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
<i>A. marowynensis</i> (Went) P. Royen	Guy., Su.	(2)	2	VU	Schnell (1969), Werkhoven & Peeters (1993)
<i>A. membranacea</i> Tul.	Br.	1	1	DD	
<i>A. minor</i> P. Royen	Br.	1	1	DD	
<i>A. multibranchiata</i> (Matthiesen) P. Royen	Ve.	1	4	LC	Velásquez (1994), Berry (2004)
<i>A. nana</i> Went	Su., Ve.	n.a.	7	LC	Werkhoven & Peeters (1993), Appendix 1
<i>A. parvifolia</i> P. Royen	Br.	1	1	DD	
<i>A. penicillata</i> (P. Royen) P. Royen	Su.	1	3	VU	Werkhoven & Peeters (1993)
<i>A. peruviana</i> (Wedd.) Engl.	Ec., Pe.	1	2	CR B1a,b(iii)	scored by León (2006) Hollander & Berg (1983)
<i>A. petiolata</i> Hollander	Su.	n.a.	1	DD	
<i>A. pilgeri</i> Mildbr.	Br., Su.	2	2	DD	
<i>A. platystigma</i> P. Royen	Br.	1	1	DD	
<i>A. psyllophora</i> Tul. & Wedd.	Br.	1	1	DD	
<i>A. pusilla</i> Tul.	Guy.	1	1	DD	
<i>A. pygmaea</i> Tul.	Br.	1	1	DD	
<i>A. rangiferina</i> P. Royen	Br.	1	1	DD	

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>A. richardiana</i> (Tul.) P. Royen	Fr. Gu., Guy., Su., Ve.	> 20	> 20	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Philbrick (2002), Berry (2004)
<i>A. riedelii</i> Tul.	Br.	(6)	(6)	LC	
<i>A. ruppioides</i> Tul.	Co., Ve.	1	3	VU	Velásquez (1994), Berry (2004)
<i>A. secundiflora</i> Pulle	Guy., Su.	(2)	(3)	VU	Schnell (1969), Werkhoven & Peeters (1993)
<i>A. spruceana</i> (Wedd.) Engl.	Br.	1	1	DD	
<i>A. staheliana</i> (Went) P. Royen	Guy., Su., Ve.	(5)	> 15	LC	Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
<i>A. surumuensis</i> (Engl.) P. Royen	Br., Guy., Su.	(3)	(3)	VU	
<i>A. tenuifolia</i> P. Royen	Br.	1	1	DD	
<i>A. treslingiana</i> (Went) P. Royen	Su.	(4)	(4)	LC	Werkhoven & Peeters (1993)
<i>A. versteegiana</i> (Went) P. Royen	Su.	2	2	VU	Werkhoven & Peeters (1993)
<i>A. yguazuensis</i> Chodat & Vischer	Ar.	1	1	VU	Tur (1997)
<i>Castelnavia cuneifolia</i> P. Royen [see <i>C. princeps</i>]	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
<i>C. fimbriata</i> Tul. & Wedd. [see <i>C. multipartita</i>]	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
<i>C. fluitans</i> Tul. & Wedd.	Br.	1	7	LC	Philbrick et al. (2009)
<i>C. lindmaniana</i> Wurm.	n.a.	1	n.a.	n.a.	Philbrick et al. (2009)
<i>C. monandra</i> Tul. & Wedd.	Br.	1	1	CR	Philbrick et al. (2009)
<i>C. multipartita</i> Tul. & Wedd.	Br.	1	9	LC	Philbrick et al. (2009)
<i>C. noveloi</i> C. T. Philbrick & C. P. Bove	Br.	n.a.	1	CR	Philbrick & Bove (2008), Philbrick et al. (2009)
<i>C. princeps</i> Tul. & Wedd.	Br.	(8)	11	LC	Philbrick et al. (2009)
<i>C. pusillima</i> Tul. & Wedd. [see <i>C. fluitans</i>]	n.a.	1	n.a.	n.a.	
<i>C. serpens</i> Tul. & Wedd. [see <i>C. fluitans</i>]	n.a.	1	n.a.	n.a.	
<i>Ceratolacis erythrolichen</i> (Tul. & Wedd.) Wedd.	Br.	1	1	CR B1b(iii)	Philbrick et al. (2004b)
<i>C. pedunculatum</i> C. T. Philbrick, Novelo & Irgang	Br.	n.a.	4	VU	Philbrick et al. (2004b)
<i>Cipoia inserta</i> C. T. Philbrick, Novelo & Irgang	Br.	n.a.	13	LC	Philbrick et al. (2004a), Appendix 1
<i>C. ramosa</i> C. P. Bove, C. T. Philbrick & Novelo	Br.	n.a.	1	CR	Bove et al. (2006)
<i>Devillea flagelliformis</i> Tul. & Wedd. [see <i>Podostemum flagelliforme</i>]	Br.	1	n.a.	n.a.	Philbrick & Novelo (2004)
<i>Diamantina lombardii</i> Novelo, C. T. Philbrick & Irgang	Br.	n.a.	3	VU	Philbrick et al. (2004a), Appendix 1
<i>Jenmaniella ceratophylla</i> Engl.*	Guy.	2	(7)	LC	Velásquez (1994), Berry (2004)
<i>J. fimbriata</i> P. Royen	Br.	1	2	VU	
<i>J. guianensis</i> Engl.	Guy.	(1)	(1)	DD	
<i>J. isoetifolia</i> P. Royen	Guy.	1	1	DD	
<i>J. jenmanii</i> (Engl.) P. Royen	Guy.	2	2	DD	

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ³	IUCN ³	Source
<i>J. tridactylifolia</i> Engl.	Guy.	2	(2)	DD	
<i>J. varians</i> Engl.	Br., Guy.	4	4	DD	
<i>Lonchostephus elegans</i> Tul.	Br.	1	3	VU	Appendix 1
<i>Lophogyne arcuifera</i> Tul. & Wedd. [see <i>Lophogyne</i> sp. A]	n.a.	(8)	n.a.	n.a.	Bove et al., in press
<i>L. helicandra</i> Tul. [see <i>Lophogyne</i> sp. A]	n.a.	(4)	n.a.	n.a.	Bove et al., in press
<i>Lophogyne</i> sp. A	Br.	n.a.	10	VU	Bove et al., in press
<i>Macarenia clavigera</i> P. Royen	Co.	1	(1)	VU	
<i>Marathrum aeruginosum</i> P. Royen	Ve.	1	2	VU	Velásquez (1994), Berry (2004)
<i>M. azarensis</i> Tur	Ar.	n.a.	1	VU	Tur (2003)
<i>M. capillaceum</i> (Pulle) P. Royen	Fr. Gu., Guy., Su., Ve.	3	(7)	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004)
<i>M. cheiriferum</i> P. Royen [see <i>M.</i> <i>oxycarpum</i>]	n.a.	(6)	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
<i>M. cubanum</i> C. Wright	Cu.	(2)	2	DD	
<i>M. elegans</i> P. Royen [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	3	n.a.	n.a.	Novelo & Philbrick (1997), Novelo et al. (2009)
<i>M. foeniculaceum</i> Humb. & Bonpl.	Be., Co., C.R., Ec., Gua., Ho., Me., Ni., Pa.	(6)	> 25	LC	Burger (1983), Novelo et al. (2009)
<i>M. haenkeanum</i> Engl. [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	(4)	n.a.	n.a.	Novelo & Philbrick (1997), Novelo et al. (2009)
<i>M. leptophyllum</i> P. Royen [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	1	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
<i>M. minutiflorum</i> Engl.* [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	(14)	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
<i>M. oxycarpum</i> Tul. [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	(7)	n.a.	n.a.	Burger (1983), Novelo et al. (2009)
<i>M. pauciflorum</i> Tul.*	Guy.	(3)	(3)	VU	
<i>M. pusillum</i> P. Royen [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	1	n.a.	n.a.	
<i>M. rubrum</i> Novelo & C. T. Philbrick [see <i>M. foeniculaceum</i>]	n.a.	n.a.	n.a.	n.a.	Novelo & Philbrick (1993a, 1997), Novelo et al. (2009)
<i>M. schiedeanum</i> Cham. [see <i>M.</i> <i>foeniculaceum</i>]	n.a.	> 20	n.a.	n.a.	Burger (1983), Novelo & Philbrick (1997), Novelo et al. (2009)
<i>M. squamosum</i> Wedd.*	Br., Ve.	2	(6)	LC	Velásquez (1994), Berry (2004)
<i>M. stenocarpum</i> (Wedd.) P. Royen [see <i>M. foeniculaceum</i>]	n.a.	3	n.a.	n.a.	Burger (1983)
<i>M. striatifolium</i> P. Royen	Pe.	1	1	CR B1a,b(iii)	scored by León (2006)
<i>M. tenue</i> Liebm.	C.R., Gua., Me.	> 15	> 20	LC	Burger (1983), Novelo & Philbrick (1997)
<i>M. trichophorum</i> P. Royen	Me.	(2)	n.a.	n.a.	rejected name; Novelo & Philbrick (1997)

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>M. utile</i> Tul.	Co., C.R., Ho., Ve.	(10)	> 20	LC	Burger (1983), Berry (2004), Appendix 1
<i>Mniopsis erulsiana</i> Warm.	n.a.	1	n.a.	n.a.	dubious species; Philbrick & Novelo (2004)
<i>M. glazioviana</i> Warm. [see <i>Podostemum ovatum</i>]	n.a.	7	n.a.	n.a.	
<i>M. saldanhana</i> Warm. [see <i>Podostemum saldanhanum</i>]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
<i>M. scaturigina</i> Mart. [see <i>Podostemum scaturiginum</i>]	n.a.	(9)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>M. weddelliana</i> Tul.* [see <i>Podostemum weddellianum</i>]	n.a.	(12)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>Monostylis capillacea</i> Tul.	Bo., Br.	1	10	LC	Appendix 1
<i>Mourera alcornis</i> (Tul.) P. Royen	Br., Ve.	2	3	VU	Rial & Bove (2007)
<i>M. aspera</i> (Bong.) Tul.*	Br.	(13)	(11)	LC	
<i>M. fluviatilis</i> Aubl.	Br., Guy., Su., Ve.	> 25	> 25	LC	Schnell (1969), Velásquez (1994), Berry (2004)
<i>M. glazioviana</i> Warm.	Br.	1	1	DD	
<i>M. schwackeana</i> Warm.	Br.	2	2	DD	
<i>M. weddelliana</i> Tul.	Br.	2	(2)	VU	
<i>Oserya biceps</i> Tul. & Wedd.	Br.	1	1	DD	
<i>O. coulteriana</i> Tul.	Me.	(3)	> 20	LC	Novelo & Philbrick (1997)
<i>O. flabellifera</i> Tul. & Wedd.	Br.	1	1	DD	
<i>O. longifolia</i> Novelo & C. T. Philbrick	Me.	n.a.	1	VU	Novelo & Philbrick (1995, 1997)
<i>O. minima</i> P. Royen	Su.	1	1	DD	Werkhoven & Peeters (1993)
<i>O. perpusilla</i> (Went) P. Royen	Guy., Su., Ve.	5	7	LC	Schnell (1969), Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004), Appendix 1
<i>O. sphaerocarpa</i> Tul.	Guy.	1	1	DD	
<i>Podostemum aguirens</i> Chodat & Vischer [see <i>P. distichum</i>]	n.a.	3	n.a.	n.a.	
<i>P. atrichum</i> Chodat & Vischer [see <i>P. distichum</i>]	n.a.	2	n.a.	n.a.	
<i>P. ceratophyllum</i> Michx.*	N.A., Do., Ho.	> 50	> 50	LC	Philbrick & Novelo (2004)
<i>P. comatum</i> Hicken	Ar., Br., Par., Ur.	1	13	LC	Philbrick & Novelo (2004)
<i>P. dentatum</i> P. Royen [see <i>P. muelleri</i>]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. dimorphum</i> P. Royen [see <i>P. comatum</i>]	n.a.	1	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. distichum</i> (Cham.) Wedd.	Ar., Br., Par., Ur.	(4)	> 25	LC	Philbrick & Novelo (2004)
<i>P. flagelliforme</i> (Tul. & Wedd.) C. T. Philbrick & Novelo	Br.	1	1	CR B1b(iii)	Philbrick & Novelo (2004)
<i>P. fruticosum</i> (Tul. & Wedd.) Wedd.	Br.	1	n.a.	n.a.	dubious species; Philbrick & Novelo (2004)

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>P. galvone</i> Warm. [see <i>P. muelleri</i>]	n.a.	(3)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. glaziovianum</i> Warm. [see <i>P. distichum</i>]	n.a.	(1)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. irgangii</i> C. T. Philbrick & Novelo	Br.	n.a.	2	VU	Philbrick & Novelo (2001, 2004)
<i>P. muelleri</i> Warm.	Ar., Br., Ur.	(5)	> 20	LC	Philbrick & Novelo (2004)
<i>P. ostenianum</i> Warm. [see <i>P. rutifolium</i> subsp. <i>rutifolium</i>]	n.a.	(3)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. ovatum</i> C. T. Philbrick & Novelo	Br.	7	7	LC	Philbrick & Novelo (2004)
<i>P. ricciiforme</i> (Liebm.) P. Royen [see <i>P. rutifolium</i> subsp. <i>ricciiforme</i>]	n.a.	2	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. rutifolium</i> Warm. subsp. <i>rutifolium</i>	Ar., Br., Par., Ur.	4	> 45	LC	Philbrick & Novelo (2004)
<i>P. rutifolium</i> subsp. <i>ricciiforme</i> (Liebm.) Novelo & C. T. Philbrick	Be., Me., Co., C.R.	n.a.	> 20	LC	Philbrick & Novelo (2004)
<i>P. saldanhanum</i> (Warm.) C. T. Philbrick & Novelo	Br.	1	4	VU	Philbrick & Novelo (2004)
<i>P. scaturiginum</i> (Mart.) C. T. Philbrick & Novelo	Br.	9	12	LC	Philbrick & Novelo (2004)
<i>P. schenkii</i> Warm. [see <i>P. distichum</i>]	n.a.	(10)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. undulatum</i> P. Royen* [see <i>P. comatum</i>]	n.a.	(5)	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. uruguayense</i> Warm. [see <i>P. muelleri</i>]	n.a.	2	n.a.	n.a.	Philbrick & Novelo (2004)
<i>P. weddellianum</i> (Tul.) C. T. Philbrick & Novelo	Br.	(10)	> 40	LC	Philbrick & Novelo (2004)
<i>Rhyncholacis apiculata</i> P. Royen	Guy.	3	3	VU	Velásquez (1994), Berry (2004)
<i>R. applanata</i> K. I. Goebel*	Guy., Ve.	1	(6)	LC	
<i>R. brassicifolia</i> P. Royen	Co.	1	1	DD	Velásquez (1994), Berry (2004)
<i>R. brevistamina</i> P. Royen	Guy.	2	(2)	VU	
<i>R. carinata</i> P. Royen	Br.	1	1	DD	
<i>R. coronata</i> P. Royen	Guy., Ve.	1	2	VU	
<i>R. crassipes</i> Spruce ex Wedd.	Br.	2	2	DD	Werkhoven & Peeters (1993)
<i>R. cristata</i> P. Royen	Su.	1	(2)	VU	
<i>R. dentata</i> P. Royen	Su.	2	2	VU	Werkhoven & Peeters (1993)
<i>R. divaricata</i> Matthiesen	Ve.	1	4	LC	Velásquez (1994), Berry (2004)
<i>R. flagellifolia</i> P. Royen	Ve.	3	(5)	VU	Berry (2004)
<i>R. guyanensis</i> P. Royen	Guy.	1	1	DD	Velásquez (1994), Berry (2004)
<i>R. hydrochorium</i> Tul.	Guy., Ve.	(3)	(6)	LC	
<i>R. jenmanii</i> Engl.*	Guy.	3	(5)	LC	Velásquez (1994)
<i>R. linearis</i> Tul.	Br., Guy., Ve.	2	(3)	VU	
<i>R. minor</i> P. Royen	Br.	1	1	DD	Berry (2004)
<i>R. nitelloides</i> (Wedd.) P. Royen	Br.	1	1	DD	
<i>R. nobilis</i> P. Royen	Co.	(1)	1	DD	
<i>R. oligandra</i> Wedd.*	Br., Ve.	1	(3)	VU	

APPENDIX 2. Continued.

Species	Country ¹	No. of rivers: Royen ²	No. of rivers: Current ²	IUCN ³	Source
<i>R. penicillata</i> Matthiesen	Ve.	1	6	LC	Velásquez (1994), Berry (2004)
<i>R. unguifera</i> P. Royen	Br.	1	1	DD	
<i>R. varians</i> Spruce ex Wedd.*	Br.	2	(2)	VU	
<i>Tristicha trifaria</i> (Bory ex Willd.) Spreng.	widespread	> 25	> 50	LC	Burger (1983), Cusset & Cusset (1988), Velásquez (1994), Novelo & Philbrick (1997), Berry (2004)
<i>Tulasneantha monadelpha</i> (Bong.) P. Royen	Br.	(1)	(1)	VU	
<i>Vanroyenella plumosa</i> Novelo & C. T. Philbrick	Me.	n.a.	2	VU	Novelo & Philbrick (1993b)
<i>Weddellina squamulosa</i> Tul.*	Br., Co., Guy., Su., Ve.	(10)	> 25	LC	Werkhoven & Peeters (1993), Velásquez (1994), Berry (2004), Appendix 1
<i>Wettsteinola accorsii</i> (Toledo) P. Royen	Br.	1	1	CR B1b(iii)	V. Bittrich, pers. comm.
<i>W. apipensis</i> Tur	Ar.	n.a.	1	CR B1b(iii)	Tur (1975, 1997)
<i>W. pinnata</i> Suess.	Br.	1	1	DD	

Abbreviations: Ar., Argentina; Be., Belize; Bo., Bolivia; Br., Brazil; Co., Colombia; C.R., Costa Rica; Cu., Cuba; Do., Dominican Republic; Ec., Ecuador; Fr. Gu., French Guiana; Gua., Guatemala; Guy., Guyana; Ho., Honduras; Me., Mexico; N.A., North America; n.a., not applicable; Ni., Nicaragua; Pan., Panama; Par., Paraguay; Pe., Peru; Su., Suriname; Ur., Uruguay; Ve., Venezuela.

* Species in which infraspecific taxa are recognized but not listed here.

¹ Country is listed only for species recognized in the current taxonomy.

² Number of rivers in parentheses are estimates.

³ For explanation of IUCN assessment categories, see IUCN (2009).

APPENDIX 3. The distribution of 22 representative species and two taxonomic forms in each of five hydrographic regions or major areas as demarcated by Ziesler and Ardizzone (1979). Within each hydrographic region or major area, the river systems and rivers that each taxon is documented from are indicated with a numeral one. The last column lists the total species documented from each river.

Region	River System	River	<i>Castelnavia fluitans</i>	<i>Castelnavia monandra</i>	<i>Castelnavia multipartita</i> f. <i>multipartita</i>	<i>Castelnavia multipartita</i> f. <i>pendulosa</i>	<i>Castelnavia novaei</i>	<i>Castelnavia princeps</i>	<i>Ceratolacis pedunculatum</i>	<i>Cipoiia inserta</i>	<i>Cipoiia ramosa</i>	<i>Diamantina lombardii</i>	<i>Lophogyne</i> sp. A	<i>Monostylis capillacea</i>	<i>Podostemum comatum</i>	<i>Podostemum distichum</i>	<i>Podostemum flagelliforme</i>	<i>Podostemum irgangii</i>	<i>Podostemum muelleri</i>	<i>Podostemum ovatum</i>	<i>Podostemum rutifolium</i> subsp. <i>rutifolium</i>	<i>Podostemum saldanhannum</i>	<i>Podostemum scaturiginum</i>	<i>Podostemum weddellianum</i>	<i>Weddellina squamulosa</i>	Species per river	
Amazon River System	Cumina	Cumina																								1	1
		Japurá																								1	1
		Uatumã																								1	1
	Madeira	Apiacás	1												1											1	3
		Aripuanã	1	1	1										1											1	5
		Guariba	1	1																						2	
		Jamari													1											1	
		Juruena							1						1											2	
		Pacáas Novos																								1	1
		Roosevelt	1	1											1											1	4
		Uaupés																								1	1
		Itenez													1											1	
		(Guaporé)																								1	3
		Juruena	1						1																	1	
		Nobres							1																	1	5
		Teles Pires	1	1	1										1											1	4
		São Benedito			1	1			1																	1	
		Tapajós													1											4	
	Tocantins	Araguaia	1	1					1									1								1	2
		Bonito							1																	1	1
		Cachoeirinha																								1	
		Cobras									1															1	
		Couros									1												1			2	
		Das Almas									1															1	2
		Lajeado													1									1		1	
		Macaco																								1	1
		Matrinchã																								1	1
		Peixe																								1	
	Trombetas	Preto									1															1	1
		Ribeirão Monte																								1	
		São Patrício			1											1										2	
		Taquaruçu					1																	1		1	
		Uru																								1	1
		Cachorro																								1	1
		Paru do Oeste																								1	1
		Total rivers	7	1	6	3	1	6	0	4	0	0	0	10	0	0	1	0	0	1	0	0	0	3	0	19	

1000

Region	River System	River																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																																							
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APPENDIX 3. Continued.

Region	River System	River	<i>Castelnavia fluitans</i>	<i>Castelnavia monandra</i>	<i>Castelnavia multipartita</i> f. <i>multipartita</i>	<i>Castelnavia multipartita</i> f. <i>pendulosa</i>	<i>Castelnavia noveboracensis</i>	<i>Castelnavia princeps</i>	<i>Ceratolacis pedunculatum</i>	<i>Cipicia inserta</i>	<i>Cipicia ramosa</i>	<i>Diamantina lombardii</i>	<i>Lophogyne</i> sp. A	<i>Monostylis capillacea</i>	<i>Podostemum comatum</i>	<i>Podostemum distichum</i>	<i>Podostemum flagelliforme</i>	<i>Podostemum virgatum</i>	<i>Podostemum muelleri</i>	<i>Podostemum ovatum</i>	<i>Podostemum ruifolium</i> subsp. <i>ruifolium</i>	<i>Podostemum saldianhanum</i>	<i>Podostemum scaturiginum</i>	<i>Podostemum weddellianum</i>	<i>Weddellina squamulosa</i>	Species per river
S	S	Bicudo					1	1																		2
		Cipó							1															1		2
		Corrente							1	1	1															3
		Imbaiaçã							1																	1
		Pará							1														1			2
		Paraúna							1																	1
		Paraopeba							1																	1
		Picão						1	1																	2
		Santo Antônio																					1			1
		São Bento																					1			1
		Verde																					1			1
	S	Aldeia Velha											1											1		2
		Pelotas																						1		1
		Quartéis																						1		1
		São João																						1		1
	S	Taquari																						1		1
	S	Soberbo																						1		1
		Das Pedras																			1					1
	V	Cachoeira da																			1					
		Gruta da																								
		Oneça											1													1
		Preto																						1		1
		Timbui																						1	34	0
		Total rivers	0	0	0	0	0	2	4	9	1	3	10	0	0	0	0	0	0	7	0	3	6	34	0	
G	A	Toekoemoetoe																								1
		Essequibo																								1
		Potaro																								1
		Puruni																								1
		Nickerie																								1
		Oyapock																								1
		Saramacca																								1
		Suriname																								1
O	R	Total rivers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	8	
		Caroní																								1
		Cataniapo																								1
		Cuao																								1
		Orinoco																								1
		Ventuari																								5
P	R	Total rivers	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	0	5	
		Caracol														1										1
		Pinto														1										1
		Santa Cruz														1										1
		Apiúna																	1		1					2

[illegible]

Region	River System	River	<i>Castelnavia fluitans</i>	<i>Castelnavia monandra</i>	<i>Castelnavia multipartita</i> f. <i>multipartita</i>	<i>Castelnavia multipartita</i> f. <i>pendulosa</i>	<i>Castelnavia noveloi</i>	<i>Castelnavia princeps</i>	<i>Ceratolacis pedunculatum</i>	<i>Cipoia inserta</i>	<i>Cipoia ramosa</i>	<i>Diamantina lombardii</i>	<i>Lophogyne</i> sp. A	<i>Monostylis capillacea</i>	<i>Podostemum comatum</i>	<i>Podostemum distichum</i>	<i>Podostemum flagelliforme</i>	<i>Podostemum irgangii</i>	<i>Podostemum muelleri</i>	<i>Podostemum ovatum</i>	<i>Podostemum rutifolium</i> subsp. <i>rutifolium</i>	<i>Podostemum saldanhanum</i>	<i>Podostemum scaturiginum</i>	<i>Podostemum weddellianum</i>	<i>Weddellina squamulosa</i>	Species per river
Cubatão*	Forqueta	Cubatão																								1
		Forqueta																								1
		Chuvisqueiro																								2
Itajaí*	Cononito	Atroio do Cononito																								1
		Itajaí																								4
		Itajaí-Açu																								2
		Itajaí do Norte																								1
		Itajaí do Oeste																								1
		São Luis																								1
		Tafona																								1
		Unknown river																								2
Jacu*	Jacu	name																								1
		Vacacaí																								1
		Jaguarião*																								1
Jacu*	Jacu	Jaguarião																								1
		Francisco																								1
		Alves																								1
Lagoa dos Patos*	Lagoa dos Patos	Quilombo																								1
		Lagoa dos Patos																								1
		Pinto																								1
Paraguay Paraná	Paraguay Paraná	Paraguay																								1
		Acaray																								1
		Ainrucca																								1
		Apa																								1
		Bonito																								1
		Capitoni																								1
		Capitanga																								2
		Capivari																								1
		Cetvo																								1
		Corumbá																								1
		Cumapiru																								1
		Ignacu																								3
		Leopoldo de Bulhões																								1
Paraná	Padre Souza	Padre Souza																							1	
		Dos Patos																							1	
		Peixe																							1	
		Piracicaba																							2	
		Piray Guazu																							2	
		Pirai Mirim																								1
		Piribebuy																							1	

APPENDIX 3. Continued.

Region	River System	River	<i>Castelnavia fluitans</i>	<i>Castelnavia monandra</i>	<i>Castelnavia multipartita f. multipartita</i>	<i>Castelnavia multipartita f. pendulosa</i>	<i>Castelnavia noveloi</i>	<i>Castelnavia princeps</i>	<i>Ceratolacis pedunculatum</i>	<i>Cipoia inserta</i>	<i>Cipoia ramosa</i>	<i>Diamantina lombardii</i>	<i>Lophogyne</i> sp. A	<i>Monostylis capillacea</i>	<i>Podotemum comatum</i>	<i>Podotemum distichum</i>	<i>Podotemum flagelliforme</i>	<i>Podotemum irgaugii</i>	<i>Podotemum muelleri</i>	<i>Podotemum ovatum</i>	<i>Podotemum rutifolium</i> subsp. <i>rutifolium</i>	<i>Podotemum saldanhanum</i>	<i>Podotemum scaturiginum</i>	<i>Podotemum weddellianum</i>	<i>Weidellina squamulosa</i>	Species per river
		Ribeirão dos Dias																						1	1	
		San Ignacio Sapucaí Grande																		1				1	1	
		Tabay														1			1						1	
		Tebicuary													1	1									1	
		Trindade														1									1	
		Verde						1								1								1	2	
		Unknown river name														1								1	2	
Piratini*		Lajeado													1	1			1	1					4	
Ribeira do Iguape*		Iguape																		1					1	
Sinos*		Chuvisqueiro														1									1	
		Unknown														1									1	
Taquari*		Antas														1				1					2	
		Camisa														1		1	1	1					3	
		Fao																		1					1	
		Forquetinha														1				1					2	
		Moraes																		1					1	
		Arroio Tatim														1									1	
		Tijela																		1					1	
		Unknown river name																							1	
Tubarão*		Tubarão														1					1				1	
Uruguay		Barra Grande																		1					1	
		Burica																		1					2	
		Butia														1					1				2	
		Castilhos													1						1				4	
		Chapecó														1	1				1				3	
		Chapecozinho																			1				1	
		Chimiray																	1	1					2	
		Conceição																	1	1					2	
		Engano																		1					1	
		Garabi																			1				1	
		Guarita													1	1					1				4	
		Irani														1					1				2	
		Jacutinga																		1	1				2	
		Jaguari																			1				1	
		Lageado														1				1	1				3	
		Paraíso																			1				1	
		Pardo													1					1	1				1	
		Pelotas																		1	1				3	

APPENDIX 3. Continued.

Region	River System	River	<i>Castelnavia fluitans</i>	<i>Castelnavia monandra</i>	<i>Castelnavia multipartita</i> f. <i>multipartita</i>	<i>Castelnavia multipartita</i> f. <i>pendulosa</i>	<i>Castelnavia noveloi</i>	<i>Castelnavia princeps</i>	<i>Ceratolacis pedunculatum</i>	<i>Cipoia inserta</i>	<i>Cipoia ramosa</i>	<i>Diamantina lombardii</i>	<i>Lophogyne</i> sp. A	<i>Monostylis capillacea</i>	<i>Podostemum comatum</i>	<i>Podostemum distichum</i>	<i>Podostemum flagelliforme</i>	<i>Podostemum irangii</i>	<i>Podostemum muelleri</i>	<i>Podostemum ovatum</i>	<i>Podostemum ruifolium</i> subsp. <i>ruifolium</i>	<i>Podostemum saldanhanum</i>	<i>Podostemum scutigerinum</i>	<i>Podostemum weddellianum</i>	<i>Weddellina squamulosa</i>	Species per river
		Pepiri-Guazu													1	1										2
		Poco													1	1										2
		Porongo																			1					1
		São João														1										1
		Surubim																			1					1
		Suzana														1			1							2
		Taimbezinho														1										1
		Taquarembó													1						1					2
		Teixeira Soares														1		1			1					3
		Turvo																1	1		1					2
		Urucúá													1											1
		Uruguay																	1	1						2
		Vacacáí																	1							1
		Vacutinga																	1		1					2
		Várzea																			1					1
		Vietnan														1										1
		Lageado Grande													1						1					2
		Unknown river name																			1					1
		Total rivers	0	0	0	0	0	3	0	0	0	0	0	0	13	44	0	2	33	0	47	0	3	6	0	

* River systems in the Paraná River System hydrographic region that drain directly into the Atlantic Ocean or coastal lakes, i.e., not into the Paraná River drainage basin.